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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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Soils and Agriculture of the Palau Islands[1]

A. J. Vessel and Roy W. Simonson[2]

Soils of the Palau Islands range from deeply weathered Latosols[3] to shallow, rocky Lithosols, and include Regosols, Alluvial Soils, and Organic Soils. Most extensive in the islands are the Latosols, of general interest because of their wide distribution in the humid tropics. Associated soils are much less extensive but are more important to local food production. The latter also illustrate effects of local factors in soil formation. Data on characteristics, distribution, and utilization of the soils and a preliminary evaluation of their agricultural potentialities are given in this paper. More complete descriptions of the soils are part of a comprehensive report on the geology and soils of the islands now being prepared for publication as a professional paper of the U. S. Geological Survey.

GEOGRAPHIC SETTING

Location and Extent

Most western group of the Caroline Islands, the Palau chain is almost directly south of Tokyo and due east of Mindanao. Location of the group in the western Pacific Ocean is shown in Figure 1. Lying 7° north of the equator, the Palaus are in the same latitude as Colombia and Venezuela.

The Palau chain stretches approximately 50 miles, from Kayangel at the north to Angaur at the south. From east to west, the dimensions of the chain range from 3 to 25 miles, as measured to the outer barrier reefs.

The total land area of the group, which consists of some 350 closely spaced islands and islets, is 175 square miles. Babelthuap, largest island in the group, has an area of almost 140 square miles. The bulk of the remaining land area is distributed among eight additional islands. Most of the 350 islands and islets of the chain are tiny reefs or bars, barely above sea level.

Physiography and Topography

The four types of islands in the Palau group are reef and atoll islands, platform islands, high limestone islands, and volcanic islands (Tayama, 1953). The reef and atoll islands, by far the most numerous, are flat land surfaces only a few feet above sea level. Examples of this type are Kayangel atoll at the north end of the chain and the many small unnamed reefs and atolls north of Peleliu. The platform islands, also mainly flat, are a little higher than the reefs and atolls. Angaur and Peleliu are chiefly of this type, though part of each consists of limestone ridges. The high limestone islands rise steeply out of the sea and are mostly narrow and elongated in shape. A few have the form of mushrooms. The principal high limestone islands are Urukthapel and Eil Malk; these and the numerous small ones all lie between Koror and Peleliu, approximately 25 miles apart. Parts of

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[1] A reconnaissance soil survey of the islands was made in 1948 as a part of a cooperative program of soil and geological mapping of islands in the western Pacific Ocean carried out cooperatively by the Corps of Engineers, U. S. Army, and U. S. Geological Survey, Department of the Interior. Manuscript received June 12, 1957.

[2] Soil Scientists, Soil Survey, Soil Conservation Service, U. S. Department of Agriculture. The authors were on assignment to the U. S. Geological Survey and the Corps of Engineers for the mapping of the Palau Islands.

[3] Latosol is a term proposed within the past few years to include zonal soils formerly called Laterites, Reddish-Brown Lateritic soils, and Yellowish-Brown Lateritic soils (Kellogg, 1949).

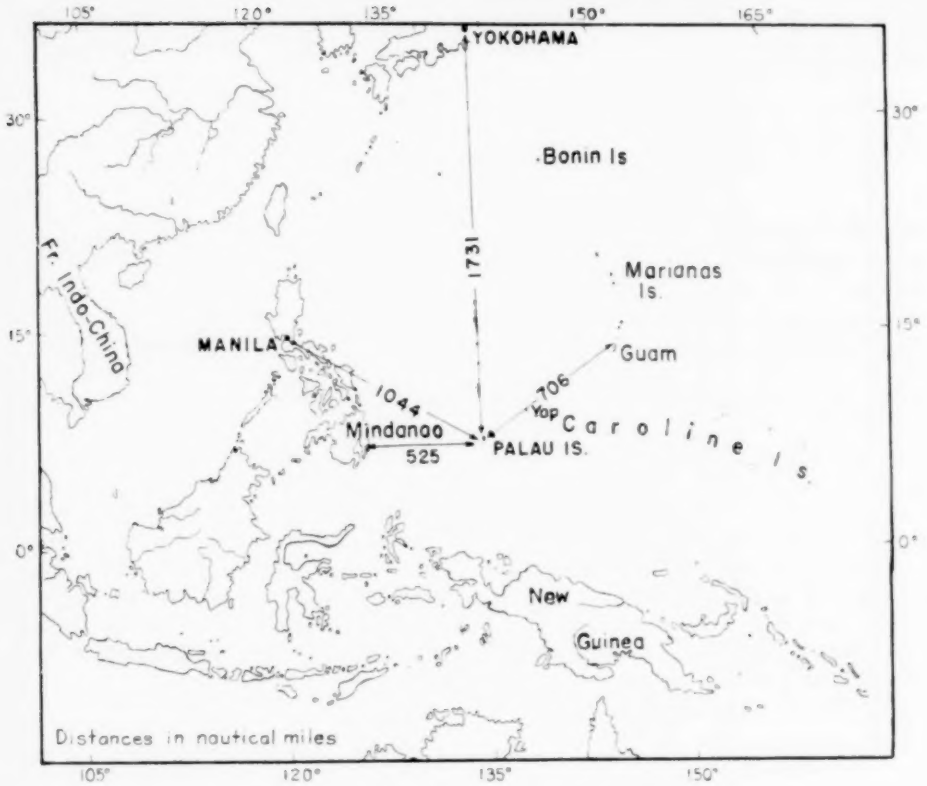

FIG. 1. Map showing the location of the Palau Islands in the western Pacific Ocean.

Peleliu, Angaur, and Koror and much of Auluptagel are also high limestone ridges. The maximum elevation of the high limestone islands is 686 feet above sea level on Urukthapel. Slopes of these islands are generally steep or very steep though a few have small central depressions with mild relief.

The volcanic islands, so named because of the underlying basement rock, are generally hilly to rolling with local relief commonly measurable in tens of feet. Slopes and ridge crests are rounded and subdued. Babelthuap has three prominent ridges running roughly parallel to the long north-south axis of the island. The highest elevation in the Palau Islands is that of 794 feet above sea level on one of the ridges in northwestern Babelthuap. The volcanic islands (Babelthuap, Arakabesan, Malakal, Auluptagel, and Koror) are all closely grouped in the northern part of the chain. As mentioned earlier, Auluptagel and Koror are partly volcanic rock and partly limestone.

Soil Parent Materials

The variety of rocks from which soils have been derived is relatively small in the Palaus. The platform and high limestone islands consist of former coral reefs. The present surface of the high limestone islands is largely a mass of rubble of assorted sizes. Much of the land surface of the platform islands also consists

of rubble, commonly small in size. The principal volcanic rocks range from olivine-augite basalts to silicic hornblende dacites (Corwin, 1951) identified as andesitic agglomerates by Japanese geologists (Tayama, 1953) and also known as basaltic and andesitic volcanic breccias. Associated with the flow rocks and agglomerates on Babelthuap are some basic volcanic tuffs. Interbedded sedimentary clays and lignite comprise the surface formations in a few places in western and southeastern Babelthuap.

The distribution of rocks on the Palau Islands is strongly reflected in the distribution of soils (Fig. 2). Rocks of volcanic origin are parent materials for most of the Latosols. Some latosolic soils have also been formed from interbedded sedimentary clays. Deep soils with distinct horizons have not been formed from limestones, most of which have rubble surfaces. Where the volcanic rocks are exposed on steep or moderately steep slopes, shallow rocky Lithosols have been formed. Deep unconsolidated materials of recent origin have given rise to Regosols, Alluvial Soils, and Organic Soils.

Climate

Typical of the humid tropics, the islands have heavy annual rainfall and high mean temperatures with small seasonal differences (U. S. Dept. of Commerce, 1953). The islands also have rather steady winds, lying as they do in the trade-wind belt. The mean annual precipitation is 148 inches, with a maximum of about 19 inches in July and a minimum of nearly 8 inches in March. On the average, at least 15 days of each month have 0.01 inch or more of rain, whereas 7 days in July have 1 inch or more. The average relative humidity is 82 per cent, with a low of 79 per cent in March and a high of 83 per cent in July, November, and December. The mean annual temperature is 81° F. The maximum and minimum mean monthly temperatures are but one degree higher and lower, whereas the diurnal variation is about ten degrees. Prevailing winds are from the northeast and east from November to June and from the south and southwest for the remainder of the year.

Vegetation

The native vegetation (Fosberg, 1946) in the Palau Islands was rain forest, which remains in only a few places on Babelthuap. The rain forest consists of large trees, including *Parinarium*, *Campnosperma*, *Couthovia*, *Cynometra*, *Dysoxylum*, *Ficus*, *Semecarpus*, *Randia*, *Fagraea*, *Pittosporum*, *Schefflera*, *Horsfieldia*, and many others. Growing also in the rain forest are such palms as *Pseudopinanga* and *Exorrhiza;* an occasional slender *Pandanus;* such climbers as *Freycinetia*, *Canavalia*, *Piper*, aroids, and *Ipomoea:* also ferns, orchids, and other epiphytes. On both the low and high limestone islands, vegetative cover consists mainly of small to medium-sized trees and shrubs because moisture conditions are unfavorable for plant growth.

The most extensive vegetative type today is anthropic savanna consisting of coarse grasses, weeds, and occasional shrubs. Common genera in the savanna are *Ischaemum*, *Paspalum*, *Digitaria*, *Miscanthus*, *Lycopodium*, *Nepenthes*, and *Pandanus* (Fosberg, 1946). Soils of extremely low fertility support almost pure stands of a fern, *Gleichenia linearis*.

SOILS

The general character and distribution of soils were determined through a reconnaissance survey, according to procedures already described (Simonson, 1953; Soil Survey Staff, 1951). This reconnaissance survey was part of a program of soil and geologic investigations in the western Pacific Ocean (Simonson, 1953). How the soils were being used was observed during the field mapping from March through August, 1948.

Distribution of the soils and land types of the islands is shown in Figure 2. The map units are either soil associations or miscel-

FIG. 2. Map showing the distribution of major soil associations and miscellaneous land types of the Palau Islands. High limestone islands and others that are not inhabited and consist of a single miscellaneous land type are not shown. Angaur and Peleliu, which are at the south end of the chain, are shown by inset maps.

laneous land types, with one exception—Shioya sand, a soil type.

Each soil association consists of one or more geographic areas with a restricted combination of soil types occurring together in a characteristic and repeating pattern. The individual soil types in each association have not been described and identified, however, as they would be in detailed surveys. The component soils in each association are classified into great soil groups or suborders.[1] Each association is then named for the dominant great soil group or suborder. The associations are described by listing the component soils

[1] The classification system followed in this paper is the one outlined by Baldwin, Kellogg, and Thorp (1938) as modified in a group of papers in *Soil Science*, Vol. 67, No. 2, February 1949, with two exceptions. The term and concept of "Latosol" as proposed by Kellogg (1949) are used. The term "Organic Soils" is used as a substitute for "Bog Soils."

and their approximate proportions. Patterns of occurrence of component soils also may be indicated. The component soils are described either by giving full morphological details for representative profiles together with data on topography and other features or by comparisons with soils that have been fully described.

Miscellaneous land types are geographic units without classifiable soils or with low proportions of such soils. Examples in the Palau Islands are smooth stony land and limestone outcrop. Stray patches of classifiable soils occur in each of these units but comprise a negligible portion of the total area.

The profile descriptions use horizon concepts and terminology as given in the *Soil Survey Manual* (Soil Survey Staff, 1951), unless otherwise stated. The identification of field textures, i.e., apparent texture as determined by the fingers when the profile was being described, is given for individual horizons. Pinholes refer to pores that are 1 mm. or less in diameter, whereas wormholes are tubular channels about 3 mm. in diameter. Numbers of pinholes, wormholes, roots, stone fragments, and concretions are indicated by three relative classes, viz., few, common, and many. Concretions are roughly spherical, unless otherwise noted, and their sizes are referred to the same limits as granular structure (see *Soil Survey Manual* for these size limits).

Each profile description is preceded by a brief statement on the geographic setting, and some are followed by comments not readily included in the description itself.

Latosols and Latosolic Soils

The Latosols are by far the most extensive soils in the Palau Islands, comprising some 60 per cent of the total land area. As shown by the map in Figure 2, they are dominant on Babelthuap, Koror, Arakabesan, and Malakal, and form the north tip of Auluptagel. Despite their large acreage, however, they have limited importance to local food production.

The Latosols of the Palaus are well drained, red to yellowish, friable, strongly acid, deep, and ferruginous or bauxitic soils derived mainly from volcanic rocks. The regoliths from volcanic rocks are weathered to great depths, but the soils do not seem to have correspondingly deep solums. The few latosolic soils formed from sedimentary clays are less deeply weathered and have shallower solums than do those derived from volcanic rocks.

These soils occur in moderately dissected uplands with a dendritic pattern of drainageways. Ridge crests are generally narrow, as are the valleys, and the intervening rounded slopes are relatively long. Local relief, i.e., differences in elevation within a unit area of approximately 160 acres (one-fourth square mile), are measurable in tens of feet, for the most part. In a few places local relief is measurable in one or two hundreds of feet, whereas in others it may be in feet.

Three associations are dominated by Latosols formed from volcanic rocks, whereas a fourth consists of latosolic soils derived from clays. Brief descriptive names are used to identify the major group in each association. Such names are not being suggested as proper names for great soil groups but are intended for local identification of the soils. When the name of an association is used as a subsection heading, it is followed by another name or names in parentheses. These names in parentheses identify the associations on the map of larger scale in the report on military geology of the islands (U. S. Department of the Army, 1956). The information on the larger map has been generalized in preparing the map in Figure 2.

1. Latosols from Breccias (Palau Association)

This association is dominated by Latosols that are red or reddish brown in the deeper profile. Colors are mainly of 2.5YR and 5YR hues[5] though a few soils are strong brown

[5] Munsell color notations. The application of this system of color notations to soils is discussed in the *Soil Survey Manual* (Soil Survey Staff, 1951).

(7.5YR hue) and a very few yellowish brown (10YR hue) below the A horizon. Bauxitic Latosols, Alluvial Soils, and Lithosols or lithosolic soils are minor components of the association. With a total area of 78 square miles, this association is much the largest in the Palau Islands. It extends from one end of Babelthuap to the other, covers all of Arakabesan and Malakal, and occupies those parts of Koror and Auluptagel underlain by volcanic rocks.

Topography is largely hilly; dominant slope gradients fall between 15 and 45 per cent. Departures from the dominant topography occur on major divides, where the uplands are undulating or gently rolling, and immediately adjacent to the valleys of large streams, where slopes are commonly steep. Hilly topography, however, dominates the association.

A profile description to illustrate the major reddish Latosols of the association follows.

(a) *Setting*. This profile was described and sampled on the island of Arakabesan about 1,000 yards west of the causeway leading to Koror. The site is about 100 feet above sea level in well-dissected uplands and has a slope of 15 per cent to the east. Vegetation in the vicinity has been disturbed by fire and by cutting, though there was little cultivation in evidence.

(b) *Profile Description*.

A_1	0-12″	Dark reddish-brown (5YR 3/4) silty clay loam, dark brown (7.5YR 3/4) when dry; weak, fine and very fine granular structure; soft, very friable; many roots; few stone fragments; strongly acid.
B_{21}	12-26″	Dark red (2.5YR 3/6) silty clay, yellowish red (5YR 4/6) when dry; compound structure of moderate fine and medium subangular blocks breaking readily to moderate fine and medium granules; slightly hard, friable, slightly plastic; roots common; few pinholes, wormholes, and stone fragments; strongly acid.
B_{22}	26-33″	Yellowish-red (5YR 4/6) silty clay, yellowish red (5YR 5/6) when dry; compound structure of moderate fine and medium angular blocks breaking readily to moderate medium and fine granules; slightly hard; friable, slightly plastic; few roots; pinholes and wormholes common; strongly acid.
B_{23}	33-39″	Comparable to B_{21} in texture, structure, and consistence but dark red (2.5YR 3/8) in color; few roots; pinholes and wormholes common; strongly acid.
C_1	39-60″	Brindled and finely variegated red, yellowish-red, pale-yellow, and light-gray (intermediate colors also present) silty clay loam; massive; soft, very friable; strongly acid.
C_2	60-102″	Similar to C_1 horizon but with lower proportions of grays in the color pattern.
C_3	102-120″	Finely variegated reddish-yellow and light-gray silty clay loam with few medium distinct mottles of weak red; massive in place but breaks out in weak coarse plates with black coatings on many faces; slightly hard, firm; strongly acid.

(c) *Additional Notes*. The identification of the B_{22} and B_{23} horizons is open to question. The B_{22} is like the adjacent ones in texture,

structure, and consistence but not in color. The differences may reflect marked banding in the original parent materials or disturbance of some kind, possibly by man. Disturbance seems probable in view of widespread occurrence of pottery fragments at some depth in Latosol profiles in the Palau Islands. Laboratory data also suggest the possibility that the present B_{23} horizon may at one time have been an A horizon, later covered by soil material of similar composition moved downslope from higher uplands.

The slope gradient at the profile site on Arakabesan falls near the lower end of the dominant range for the association as a whole. Consequently, the solum is thicker than average. It is estimated that 10 per cent of the Latosols in this association have deeper solums and that 60 per cent have slightly shallower solums, i.e., between 2 and 3 feet. The remaining 30 per cent have solum thicknesses falling between 1 and 2 feet. Regardless of variations in solum thickness the regolith is deep for all Latosols in this association, commonly ranging from 10 to 60 feet. Occasionally, thickness of the regolith may exceed 60 feet to the underlying basaltic or andesitic volcanic Breccias.

Concretionary or bauxitic Latosols, Lithosols and lithosolic soils, and Alluvial Soils comprise from 10 to 15 per cent of the association. Proportions of these three minor groups are approximately equal. The concretionary Latosols are similar to the dominant soils in the association of bauxitic Latosols from Breccias. In contrast to the Latosols, the Lithosols and lithosolic soils are formed in shallow regoliths, usually marked by rock outcrops. The Alluvial Soils occupy toe slopes and narrow valleys and are similar to those described in the subsection on Regosols, Alluvial Soils, and Organic Soils.

2. Bauxitic Latosols from Breccias (Babelthuap Association)

The dominant soils of this association are the most strongly weathered Latosols of the islands. Striking features of these soils are the large numbers of concretions on the surface and in the profile. Approximately half of the total area of this association consists of reddish, bauxitic Latosols. Most of the remainder consists of Latosols that are low or lacking in concretions, but there are also minor proportions of Lithosols or lithosolic soils and of Alluvial Soils. Much less extensive than Latosols from Breccias, this association has a total of 19 square miles, all on Babelthuap. Major areas are in the west central part of the island, though two small ones are near the south coast.

Topography is dominantly hilly. Slopes may be slightly steeper, on the average, than they are in the association of Latosols from Breccias. Local relief is commonly measurable in many tens of feet.

A profile description representative of the dominant bauxitic Latosol of the association is as follows:

(a) *Setting*. The profile was described and sampled in a former strip mine used for the extraction of bauxitic ore, approximately 1,600 yards south of Ngardmau on Babelthuap. The site has a slope of about 15 per cent to the east. Vegetation near the strip mine consists of coarse grasses and brush interspersed with almost pure stands of ferns (*Gleichenia linearis*).

(b) *Profile Description*.

A_1	0-6″	Brown (7.5YR 4/4) gravelly loam; moderate fine granular structure; soft, friable; brownish coarse and very coarse vesicular platy concretions common, few brown fine concretions; many very fine, fine, and medium roots; few small worm casts; very strongly acid.
B_2	6-18″	Red (2.5YR 4/8) silty clay; compound structure of moderate coarse subangular blocks breaking

under pressure into moderate fine and medium subangular blocks; slightly hard, friable; brown fine concretions common; few fine roots; extremely acid.

C_1 18-28″ Variegated red (2.5YR 4/8), weak red (10R 4/3), and reddish-yellow (5YR 6/8) silty clay loam; massive; slightly hard, friable; few light-gray fine concretions, few fine roots; extremely acid.

C_2 28-32″ Variegated weak red (10R 4/3), reddish-yellow (5YR 6/8), and strong brown (7.5YR 5/6) silty clay loam; massive; slightly hard, friable; few brownish coarse and very coarse concretions; few speckles of gray (N 5/); extremely acid.

C_3 32-76″ Variegated weak red (10R 4/3) and strong brown (7.5YR 5/6) gritty silty clay loam, appearing mottled because of light-gray (10YR 7/1) fine to coarse concretions; yellowish-red very coarse concretions common; extremely acid.

C_4 76-96″ Variegated weak red, strong brown, and black silty clay loam; weak coarse platy structure apparently retained from parent volcanic breccia; very strongly acid.

(c) *Additional Notes.* The concretions in the A horizon are large and tend to be roughly platy, with long axes ranging from 5 to 100 mm. and short axes from 3 to 30 mm. All seem to be vesicular, and some have shiny surfaces. Concretions are most abundant in the surface layer and in the C horizon.

The nature and distribution of concretions in the profiles of dominant Latosols in this association tend to follow certain patterns. For the most part, brown, reddish-brown, and yellowish-red concretions occur in the surface layer, though they are found at depth in some profiles. Gray and light gray concretions occur in the C horizon, especially in the upper part. Colors suggest that concretions in the deeper profile are more often low in iron oxides than those near the surface. Most concretions in the upper horizons are somewhat flattened and platy, with a few being roughly spherical. In the deeper horizons, the concretions may be platy, spherical, or assume branching cylindrical forms much like reef coral. The spherical and platy forms are most common. Total numbers of concretions are greatest in the A and C horizons, and seem to be lowest in the B horizon. Numbers of concretions decrease with increasing depth in and below the C horizon, as a rule.

Sequences and thicknesses of horizons and the degree of horizonation are not uniform among the bauxitic Latosols and related soils dominant in this association. As already indicated, these soils comprise about half of the total area of the association. Perhaps 25 per cent of the soils in this half have the horizon sequence and thicknesses as described for the one profile. Other soils either have been eroded or have failed to reach the same degree of horizon differentiation. Most of the soils have thinner A horizons than the described profile, some lack an A horizon, and others seem to have lost both A and B horizons. Some of these last-named soils have thin A horizons which seem to be in process of formation from former C horizons. Thus, about three-fourths of the bauxitic Latosols and related soils in the association have profiles somewhat like but not identical with the one described near Ngardmau. Regardless of the character of the profile, the Regolith is consistently deep, commonly exceeding 30 feet and often reaching 50 feet.

Second in extent in the association are

Latosols formed from volcanic Breccias but lacking large numbers of concretions in the profile. These soils are identical with the dominant ones in the association of Latosols from Breccias, described earlier. Some do have more concretions in the surface layer than typical, thus being intermediate in character between the bauxitic and nonbauxitic Latosols.

Lithosols or lithosolic soils and Alluvial Soils comprise 10 per cent or less of the association. The nature and distribution of these minor soils is similar in the two associations of Latosols from volcanic Breccias.

3. Latosols from Tuffs (Ngardok Association)

Although derived from different parent materials, the dominant soils of this association closely resemble the Latosols formed from volcanic Breccias, especially those low in concretions. On the whole, the soils from tuffs have thinner solums and slightly lower permeability. They have fewer concretions in the profile and seem to be less weathered than the bauxitic Latosols from Breccias. Minor components of the association are Alluvial Soils and Regosols or regosolic soils. Total area of the association is 13 square miles, which is one-fifth that of the Latosols from Breccias. Latosols from Tuffs occur only on Babelthuap, mainly in the northern half of the island.

The land surface of this soil association is highly dissected. Topography is mostly hilly to steep with local relief in many tens of feet. Ridge crests are commonly narrow but valleys are fairly broad with much fill. Occasional uplands have been dissected so as to resemble miniature Badlands, which are conspicuous though small.

A profile description to represent the Latosols from Tuffs follows.

(a) *Setting*. The profile was described and sampled south of the village of Aimeong, west central Babelthuap. The site was a 25 per cent slope to the west in uplands about 100 feet above sea level and less than 100 yards from a mangrove swamp. The vegetation at the site consisted of coarse grasses and low shrubs.

(b) *Profile Description*.

A_1	0-3″	Reddish-brown (5YR 4/4) silty clay loam; weak medium granular structure; soft, friable; many fine and medium roots, few wormholes and pinholes; strongly acid.
B	3-18″	Yellowish-red (5YR 4/8) silty clay; weak coarse and medium subangular blocky structure; slightly hard, firm, slightly plastic, slightly sticky; many fine roots; few pinholes; strongly acid.
C_1	18-42″	Bedded deposit of weathered tuffs in which the main layers are variegated weak red (10R 4/2), red (10R 4/8), pale yellow (2.5Y 7/4), and white (2.5Y 7/2) silty clay loam that is soft and friable. Intercalated layers are reddish-yellow (7.5YR 6/6) silty clay that is hard, firm, slightly sticky, and slightly plastic. The whole horizon has weak, very coarse platy structure inherited from original deposit and is strongly acid.
C	42-60″	Variegated weak red (10Y 4/2) and pale-yellow (2.5Y 7/4) silt loam with very fine white (2.5Y 8/2) specks; massive; soft, very friable; strongly acid.

Major differences among the Latosols from Tuffs are in thickness and color of solum. Approximately half of these soils have solums 1½ or more feet thick. Another fourth have solums between 1 and 1½ feet in thickness.

The remainder have solums which are less than 1 foot thick. Colors range from low chromas and values of 10R hue to rather high figures of 7.5YR hue. The bulk of the soils have colors of 2.5YR and 5YR hues. Some profiles have appreciable numbers of concretions of various sizes in and on the surface layer. Concretions may be common but not numerous. Thickness of the Regolith in which the soils are formed is generally great, commonly falling between 40 and 100 feet.

Minor components of this association, the Alluvial Soils and Regosols or regosolic soils, form 10 to 15 per cent of its total area. The Alluvial Soils are similar to those in other associations dominated by Latosols. The Regosols or regosolic soils are restricted to the steepest slopes and have about the same total area as Alluvial Soils. The Regosols or regosolic soils may have faint A horizons or may consist entirely of weathered Tuffs.

4. Latosolic Soils from Clays (Ngatpang Association and Tabagaten Association)

Two soil groups are the main components of this association, all of which are derived from sedimentary clay beds. The more extensive group consists of Red-Yellow Podzolic soils which approach Planosols in fine texture and low permeability of the B horizon. They resemble the Colbert series formed from argillaceous limestones in the southeastern United States. The B horizons are mainly yellowish-brown (10YR hue) silty clays. The second major group in the association consists of yellowish-red to red soils which seem to be intermediate in character between Latosols and Red-Yellow Podzolic soils. They have some of the properties of each. They may be more nearly related to the Davidson, Decatur, and similar series than to typical Latosols or Red-Yellow Podzolic soils. All gradations in profile exist between the yellowish-brown and red components of this association.

Minor components of the association are Low Humic-Gley soils, Alluvial Soils, and Regosols, which collectively comprise about 20 per cent of its total area. Low Humic-Gley soils occur in smooth uplands and on the lower parts of long slopes. Alluvial Soils are found along drainageways. The Regosols occupy the rare steep slopes.

Restricted in its occurrence on Babelthuap, this association has a total area of about 5 square miles. The main bodies are in the west central part of the island, with a few small ones near the southern end.

Topography is dominantly undulating to rolling, in contrast to the hilliness of the Latosols from Breccias and Tuffs. Slopes are long and gentle. Local relief is measurable in feet as a rule though it may reach tens of feet in a few places. Latosolic soils from clays comprise the smoothest uplands on Babelthuap.

5. Chemical and Mineralogical Data on Profiles

Certain laboratory analyses have been made on samples of the major horizons of several profiles from the Palau Islands. Data obtained will be given in full in a later publication, but a few are given here to complement the morphological observations. Table 1 gives data for exchangeable cations, pH, exchange capacity, base saturation, and organic matter for three profiles which represent the dominant Latosols of the islands. Table 2 gives data on chemical and mineralogical composition on a section sampled for the study of bauxite ore in an area of bauxitic Latosols.

The laboratory analyses reported in Table 1 were made in the Department of Soils and Agricultural Chemistry, University of Hawaii, and in the Soil Survey Laboratories, SCS, U. S. Department of Agriculture. Methods used at the University of Hawaii are described by Piper (1944), whereas those used in the Soil Survey Laboratories are described in U. S. Department of Agriculture Circular 757 (Peech *et al.*, 1947).

Data given in Table 2 are from the laboratories of the U. S. Geological Survey. Standard methods for chemical analysis were used

TABLE 1
EXCHANGEABLE CALCIUM AND MAGNESIUM, pH, EXCHANGE CAPACITY, BASE SATURATION, AND ORGANIC MATTER IN THREE LATOSOL PROFILES

HORIZON	DEPTH	pH	CATION EXCH. CAPACITY	EXCHANGEABLE CALCIUM	EXCHANGEABLE MAGNESIUM	BASE SATURATION	ORGANIC MATTER
	Inches		m.e./100 g	m.e./100 g	m.e./100 g	Per cent	Per cent
LATOSOL FROM BRECCIA*							
A1	0–12	5.6	22.4	8.3	1.8	45	5.20
B21	12–26	5.6	15.3	6.2	0.8	46	2.35
B22	26–33	5.8	16.7	6.6	0.7	44	2.45
B23	33–39	6.2	20.3	7.8	0.5	41	1.44
C11	39–60	6.2	13.9	7.6	0.5	58	0.50
C12	60–88	6.6	15.8	8.8	0.7	60	0.37
BAUXITIC LATOSOL FROM BRECCIA*							
A1	0–6	5.0	12.0	0.4	0.4	6	4.79
B2	6–18	5.0	8.3	0.1	0.4	7	2.38
C1	18–28	5.2	10.1	0.3	0.5	4	0.98
C2	28–34	5.2	10.2	0.3	0.6	10	0.85
C3	34–76	5.2	14.3	0.2	0.3	4	0.64
LATOSOL FROM TUFFS†							
A	0–3		36.7	7.1	5.7	37	
B	3–18		31.0	12.2	2.8	50	
C1	18–42		31.5	19.6	1.8	69	
C2	42–60		30.7	17.6	1.7	64	

* Analyses through courtesy of Dr. G. D. Sherman, Chairman, Department of Soils and Agricultural Chemistry, University of Hawaii.
† Analyses by E. M. Roller, Soil Survey Laboratories, Soil Conservation Service, U. S. Dept. of Agriculture.

in determining composition of samples given in Table 2. The quantities of gibbsite and of silicate clay minerals were estimated by Goldich from differential thermal analyses and the chemical analyses. Hematite and other minerals were obtained by difference.

6. Comparisons of Soils in Palau Islands, Hawaii, and Puerto Rico

The Latosols in the Palaus have low degrees of horizonation, diffuse horizon boundaries, and common to numerous pinholes in the profile. Morphologically, they are comparable to Latosols observed by Simonson in Hawaii, Puerto Rico, Ceylon, and Brazil. There are differences, however, among the Latosols in the Palaus as there are elsewhere. The Latosols low or lacking in concretions seem to be much less strongly weathered than are the bauxitic Latosols high in concretions. This inference is based on differences in morphology and on laboratory data given in Tables 1 and 2.

The Latosols low or lacking in concretions have A horizons that are easily recognized because they are darker and more friable than the B and C horizons. The B horizons are set apart because they are more plastic and less friable than the C horizons. Differences in plasticity are slight as indicated by dominant ranges in plastic index values (Casagrande, 1932) of 6 to 9 for the A horizons, 21 to 31 for

TABLE 2
COMPOSITION OF LAYERS FROM A DEEP SECTION THROUGH A BAUXITIC LATOSOL FROM BRECCIA NEAR NGARDMAU, BABELTHUAP*

DEPTH	SiO_2	Al_2O_3	Fe_2O_3	TiO_2	LOSS ON IGNITION	GIBBSITE	SILICATE CLAY MINERALS	HEMATITE AND OTHER MINERALS
Inches	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent
0–20	0.98	44.12	25.55	1.38	26.14	66	2	32
20–28	1.64	34.83	37.56	1.68	21.76	51	4	45
28–120	7.63	37.33	29.85	1.70	21.22	47	17	36
120–180	19.40	35.21	24.62	1.42	18.75	29	42	29

* Sampled by S. S. Goldich; hole 17, Taihei Area. Chemical analysis by Marie L. Lindberg, U. S. Geological Survey.

the B horizons, and 6 to 18 for the C horizons. The C_1 horizon of the Latosol profile described on Arakabesan has a plastic index of 31, which is in the common range for B horizons.

Morphologically, the dominant Latosols in the Palaus are like the Humic Latosols in Hawaii, described by Cline (Cline *et al.*, 1939). The profiles from breccias and tuffs are much like the Humic Latosols in the character, sequence, and thickness of horizons. Both profiles in the Palaus, however, are lower in organic matter than Humic Latosols in Hawaii, being more like the Low Humic Latosols in this feature. The profile from tuffs has exchange capacities ranging from 31 to 37 milliequivalents per 100 grams which falls within the common range of 30 to 40 milliequivalents for Humic Latosols in Hawaii. On the other hand, the profile from breccia has exchange capacities ranging from 14 to 22 milliequivalents per 100 grams which parallels the range of 15 to 30 milliequivalents for Low Humic Latosols. Ratios of exchangeable calcium to magnesium are much higher in the two profiles from the Palaus than they are in the Humic Latosols or Low Humic Latosols of Hawaii. All in all, the less weathered Latosols of the Palau Islands seem marginal between the Low Humic Latosol and Humic Latosol groups recognized in the Hawaiian Islands.

The Latosols in the Palaus also resemble those in Hawaii in low plasticity and stickiness despite high clay contents. Some Low Humic Latosols in Hawaii are 80 per cent clay but feel as though they were silty clay loams when worked between the fingers. Field textures of Latosols in the Palaus seem marginal between silty clay loam and silt loam in the A_1 horizons and between silty clay and silty clay loam in the B horizons. There is little reason to believe that the Latosols of the Palaus are lower in clay than those in Hawaii.

Latosols, though high in clay, commonly have low shrinkage values upon drying and show little or no expansion upon wetting. This behavior has been correlated with high liquid limit and low plastic index values. The liquid limits for Latosols in the Palau Islands mostly range from 56 to 82. Lower values were found in the bauxitic Latosol, which had liquid limits of 39 in the A_1 and 45 in the lower C horizons. The plastic index ranges from 6 to 31, as was indicated in an earlier paragraph. Within the continental United States liquid limit and plastic index values of similar magnitude are found in the Davidson series (Fruhauf, 1946) and similar soils, which have been classified in the Reddish-Brown Lateritic group (Simonson, 1949). Although similar to Latosols in a number of ways, the Davidson profile has a much more distinct and far less friable B horizon. Field descriptions of the Latosols in the Palaus as well as the liquid limit and plastic index values sug-

gest that these soils lean somewhat in their characteristics toward the Davidson series. Hence, they seem to be intermediate between modal profiles for the Latosol group and the Reddish-Brown Lateritic soils.

The morphology and composition of the bauxitic Latosols in the Palau Islands indicate that they are more strongly weathered than the Humic Latosols and more nearly comparable in this respect to the Humic Ferruginous Latosols of Hawaii. Sesquioxides have been concentrated to a high degree, partly in the form of concretions, in the bauxitic profiles (Table 2). Compared to the Haiku and Naiwa series in Hawaii (Cline *et al.*, 1939), the bauxitic profile is much lower in SiO_2 and TiO_2, somewhat lower in Fe_2O_3, and much higher in Al_2O_3. It is comparable in contents of SiO_2 and TiO_2, lower in Fe_2O_3, and higher in Al_2O_3 than the profiles of Nipe clay described by Marbut (1930). Thus the concentration of sesquioxides, considering both aluminum and iron, is comparable in the bauxitic Latosol to that of Humic Ferruginous Latosols of Hawaii and to the Laterite soils of Cuba and Puerto Rico. The chemical and mineralogical composition of the bauxitic profiles as indicated in Tables 1 and 2 suggests that it is one of the end products of soil formation in the humid tropics.

The Latosols of the Palau Islands clearly represent two subdivisions of the broad group or suborder. The bauxitic soils are examples of a strongly weathered group similar in many ways to the Nipe clay of Cuba and Puerto Rico and to the Humic Ferruginous Latosols of Hawaii. On the other hand, the profiles low or lacking in concretions in the Palau Islands resemble the Humic Latosols of Hawaii in some ways and the Low Humic Latosols in others. It may be that they should be considered comparable to Humic Latosols in the drier part of their climatic range. Dominant Latosols of the Palau Islands also seem to have a few properties in common with the Reddish-Brown Lateritic group of the southeastern United States.

Regosols, Alluvial Soils, and Organic Soils

These soils comprise about 6 per cent of the total land area of the Palaus but produce most of the food in the present agriculture. The one Regosol is a soil type widespread on Pacific islands, known as Shioya sand. The Alluvial Soils are moderately fine-textured and predominantly poorly drained, though they have a wide range in drainage conditions. Organic Soils consist of peats and mucks. The Alluvial Soils are slightly more extensive than either Shioya sand or the Organic Soils.

1. Shioya Sand

This soil type occupies raised beaches or low coastal terraces that are above wave action, principally in north Peleliu and at the north and south ends of Angaur. Additional areas too small to be shown in Figure 2 occur along the northeastern coast of Babelthuap and along the shores of Peleliu. Total area of Shioya sand in the islands is 2.7 square miles.

The profile of Shioya sand consists of a thin (2–3 inches) gray (2.5Y 5/1) or grayish brown (10YR 5/2) A_1 horizon over a light gray (2.5Y 7/2) C horizon. The whole profile consists of sand or fine sand, which may be replaced by gravel at depths of 2 to 4 feet. In most places, some coral fragments occur on the surface and throughout the profile. Consisting largely of coralline limestone fragments, Shioya sand is strongly calcareous.

Much of the total area of Shioya sand has been planted to coconut palms, for which the soil is well suited. Minor crops that seem to grow well are lemons, bananas, papayas, and breadfruit.

2. Alluvial Soils

These soils occur along most streams and along many of the upland drainageways in the Palau Islands. Only the areas along the lower courses of principal streams can be shown, however, in Figure 2. The soils are all slightly acid in reaction, and the dominant ones are poorly drained. Less extensive are the well-drained soils and those intermediate in

drainage. Total area of this association is slightly more than 4 square miles.

The dominant poorly-drained soils show the effects of a water table at or near the surface an important part of each year. A typical profile has a surface layer of brown (7.5YR 4/4) silty clay loam about 9 inches thick underlain by gray (5Y 5/1) or olive-gray (5Y 4/2) silty clay mottled with brownish yellow (10YR 6/8). Somewhere between 2½ and 4 feet this gives way to dark-gray, nearly impermeable clay free of mottles.

Well-drained soils in this association are commonly of similar texture but have brown surface layers grading downward into red, reddish brown, yellowish red, or yellowish brown. Mottled patterns and colors of 5Y hue are lacking in the well-drained soils. Soils with drainage intermediate between the well-drained and poorly drained ones are also intermediate in their morphology.

The Alluvial Soils are adapted to most crops that can be grown in the Palau Islands. In spite of the suitability of the soils for cultivation, however, very little of this association was being tilled in 1948. Most areas were idle, generally supporting tall coarse grasses which were replaced locally by poor forest. Taro was being grown on some patches of wet Alluvial Soils near villages. Other crops that seem to grow well on the Alluvial Soils are cassava, bananas, coconuts, and pineapples.

3. Muck and Peat

These organic soils are of major importance to present food production, despite their small total area. They occur as scattered individual bodies, mostly along the northeast coast of Babelthuap and on the islands of Angaur and Peleliu. Some bodies are too small to be shown in Figure 2. The total area of organic soils is slightly less than 3 square miles.

Muck consists of black, neutral to mildly alkaline, highly decomposed organic matter mixed with some mineral matter. Thickness of the muck commonly ranges from 2 to 3½ feet although it may be slightly less than 1 foot thick in places. The muck is generally underlain by gray silt, gray clay, or coral sand. On Angaur, all of the muck is underlain by phosphate ore in the form of pellets. Approximately 90 per cent of the total area of organic soils consists of muck.

Peat is less decayed than muck and is also commonly lower in mineral matter. Plant structures in the peat can be readily identified. The deposits range from 1 to 3½ feet in thickness over limestone or phosphate ore. The areas of peat are approximately 10 per cent of the total of Organic Soils.

The Organic Soils are especially valuable in the Palau Islands because of their suitability for taro production. They produce high yields of the crop, which is a major item in the diet of the people.

Lithosols, Stony Land, Rock Land, and Mangrove Swamp

This group comprises one soil association and three miscellaneous land types. Collectively, the group has a total area of 49 square miles, ranking second to the Latosols from Breccias. Despite their large extent, however, the Lithosols and miscellaneous land types have little usefulness to agriculture.

1. Lithosols from Volcanic Rocks

The main features of this association are the shallowness of soils, common occurrence of rock outcrops, and steep topography. Usually 6 to 15 inches deep over hard rock, the soil is dark, slightly acid, and commonly marked by a faint and thin A_1 horizon. Rock fragments are common on the surface and throughout the profile. Massive rock outcrops occur along ridge crests. The association has steep to hilly topography and is covered by forest or savanna. The steepest areas are mostly in forest, whereas the remainder is covered by coarse grasses and low shrubs with scattered pandanus trees. Restricted to Babelthuap and small nearby islands not

shown in Figure 2, this association has a total area of 7 square miles.

2. Smooth Stony Land

Smooth stony land is largely covered by limestone fragments or rubble, among which are small quantities of fine earth, usually phosphatic. For the most part, large limestone fragments are numerous enough on the surface so that a person can easily step from stone to stone. Pockets of soil material are commonly tiny but a few are as big as 1/100th of an acre. The soil material is dark brown, friable, silt loam to loamy coarse sand and may reach depths of 10 inches in some pockets. As the name of the land type suggests, smooth stony land is nearly level or very gently sloping. It forms important parts of Angaur and Peleliu and has a total area of 2½ square miles.

Most areas of smooth stony land are covered by brush and small trees. Small clearings, usually a fraction of an acre in size, are made here and there in the forest for the planting of cassava, sweet potatoes, bananas, and papayas. These may be planted separately or in mixtures, more often the latter. Individual clearings are usually abandoned to the forest again after a few crops have been produced.

3. Limestone Outcrops

This form of rock land, as its name suggests, comprises exposures of coralline limestone and rubble with little or no fine earth. The surface of the limestone is commonly pitted and pinnacled. Some soil material is present in small pockets and in crevices, generally in handfuls. Present vegetation consists of small trees and shrubs. Limestone outcrop forms the islands of Urukthapel, Eil Malk, and Ngergoe (all of which lie between Koror and Peleliu and are not shown in Figure 2); parts of Anguar, Auluptagel, Koror, and Peleliu; and the southern tip of Babelthuap. It also forms a number of small unnamed islands between Koror and Peleliu. This land type has a total area of 24 square miles, none of which is inhabited.

4. Mangrove Swamp

This miscellaneous land type comprises wooded coastal areas that are periodically flooded by salt or brackish water because of tides. The mangrove swamps occur along the coasts, on deltas, in embayments, and along the lower reaches of the streams. The main areas border the coast of Babelthuap and the eastern coast of Peleliu. Total area of mangrove swamp in the Palau Islands is slightly more than 14 square miles.

AGRICULTURE

Agricultural production in the Palau Islands in 1948 was of a subsistence type. The crops being grown were used as food for the families producing them. The main food crops were taro, cassava, and sweet potatoes. Production of these crops was by hand tillage, a clear index to the prevailing level of agricultural technology.

Crops

Taro (*Colocasia esculenta*), which yields an edible tuber, is produced mainly on Organic Soils and poorly-drained Alluvial Soils in the Palaus. It is also grown to a limited extent on Latosols, preferably on lower slopes where some seepage can be expected. Commonly grown with taro but on the outer margin of the paddies is a coarser plant (*Cyrtosperma chamissonis*) which produces a large tuber eaten when the taro crop fails. Several large "elephant ear" varieties, identified by Fosberg[6] as *Xanthosoma violacea* and *Alocasia macrorrhiza*, are grown occasionally on soils of the uplands. Like the *Cyrtosperma* in the paddies, these are also eaten only during severe food shortages.

The second crop of importance is cassava (*Manihot utilissima*), called "tapico" by the Palauans. It commonly supplements and may replace taro in the diet. The crop was introduced during German ownership of the is-

[6] Personal communication, April 9, 1951.

lands. Improved varieties with higher starch contents were brought in by the Japanese who raised cassava for export. The crop grows best during the driest season of the year, when fungus diseases are the least active. It is grown mainly on the Latosols but to some extent on Alluvial Soils.

Third in importance among food crops are sweet potatoes, which were introduced by the Spaniards. Sweet potatoes are produced by the same methods as cassava. They are grown on the Latosols, some Alluvial Soils, and Shioya sand.

Minor crops are coconuts, sugar cane, Tahitian chestnuts, breadfruit, jakfruit, pineapples, oranges, mangoes, papayas, sauersop, and pandanus. Coconut plantations were relatively important at one time but the invasion of the rhinoceros beetle has reduced production to very low levels and forced abandonment of most groves. Sugar cane, pineapples, and papayas are grown as scattered plants in a patch of cassava, sweet potatoes, or both. Orange and mango trees producing food are commonly lone plants in or near the villages, whereas chestnuts, breadfruit, jakfruit, sauersop, and pandanus grow wild in the savannas and forests.

Methods

Shifting cultivation is the general practice in the production of food crops on the Latosols of the Palau Islands. Most areas of Latosols readily accessible to villages are now in savanna vegetation. Burning of the grass is therefore the first step in clearing a garden patch. A few areas of Latosols as well as most of the smooth stony land is in forest or brush. Clearing of a garden then requires the cutting of saplings, vines, and brush, usually done with a large knife or machete. After the savanna is burned or the forest cut, the soil is stirred with a simple hoe and crops are planted.

All tillage, planting, and harvesting in the Palau Islands are done by hand. No draft animals were on the islands in 1948 nor had they been used in the past. Cultivation of the soil is by means of a four-pronged hoe introduced by the Japanese. Tillage consists of stirring of the soil to shallow depths. Subsequently, slips or seeds are planted. Vegetative reproduction by means of slips is the more common practice.

Garden patches on Latosols and some on Alluvial Soils and smooth stony land are usually planted to cassava or sweet potatoes. Some gardens may have both crops growing at the same time, plus scattered individual plants of other crop species. A single garden may be used for cassava or sweet potatoes exclusively, or the two may be alternated. After the plants become ripe they are harvested a few at a time, as needed by the family. The patch is replanted with cassava or sweet potatoes after all of one crop has been harvested. This process is then repeated until yields in that one garden patch begin to drop. Once the yields have fallen, the patch is abandoned and a new one is cleared either by fire or knife. The whole process is then repeated once more in the new clearing.

Continuous growing of taro is common practice on the Organic Soils and the poorly drained Alluvial Soils. The planting, weeding, and harvesting of taro are the responsibility of the women in the families, who also own the taro paddies. The paddies used by a single family are divided into a number of segments and planted so that one segment is always ready for harvest. Thus, the plants in different segments of one paddy may be in all stages of growth from slips that have just been placed into the soil to ripe plants awaiting harvest. After all of the plants in a given segment have been harvested, that segment is again replanted while harvest begins in another part of the paddy. Taro paddies commonly receive more attention than do upland gardens because of their greater importance in food production.

Efforts are made by the Palauans to incorporate decayed leaves and grass as well as wood ashes into the soils, especially in taro

paddies. Commercial fertilizers, insecticides, and the like, have not been available in the Palau Islands. Methods used by the Palauans to maintain and improve their soils as well as methods of tillage, planting, and harvesting are all common elements of a simple agricultural technology.

Potentialities

Improvements in agricultural technology would permit increased food production from the soils of the Palau Islands. Some improvements are possible within existing patterns of operation. For example, better crop varieties, commercial fertilizers and insecticides, and simple machinery such as hand cultivators could be used in the present agriculture. Certain shifts are thus possible without major changes in the agricultural arts. Such shifts would mean appreciable increases in food production, without realization of the full potentials of the soils.

To achieve full potential production from soils of the Palaus, major changes from the present agricultural technology would be required. What the potential may be can be inferred from current yields on Humic Latosols and Low Humic Latosols of Hawaii, soils which are comparable to those of the Palau Islands. Yields of 8 to 10 tons of sugar per acre are common on the Latosols of Hawaii (Cline *et al.*, 1939), where soil management includes heavy fertilization, irrigation, mechanization, and many more of the management elements available to agriculture in a modern industrial society. The findings of modern science and the products of modern industry are widely used for crop production on Latosols in Hawaii. Thus, the level of agricultural technology is markedly different from the one prevailing in the Palau Islands.

Experience in soil use and management does not seem directly transferable from Hawaii to the Palaus, though major soils in the two island groups are the same. The total land area and the topography of the Palaus impose certain limitations on agricultural production even with the best technology available. The small total area of the Palaus in itself restricts opportunities for the large scale agriculture in which sugar cane, cacao, and similar crops are commonly produced. Furthermore, the major soil associations of the Palau Islands are dominantly hilly to steep. Individual areas with level, undulating, or rolling topography are small. Proportions of the major soil associations with topography favorable for mechanization are therefore small. As a consequence, full use of the tools of soil management available in a modern industrial society does not promise to become feasible in the Palaus. Something less than full use of those tools is more likely to be appropriate. Possibilities for commercial agricultural production seem limited, all in all, but there is opportunity for greater food production through improvements in soil use and management.

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Pacific Area Distribution of Fresh-Water and Marine Cercarial Dermatitis[1]

GEORGE W. T. C. CHU[2]

CERCARIAL DERMATITIS, a form of "swimmer's itch," is a skin infection caused by the penetration of schistosome cercariae. The disease is also known as schistosome dermatitis. The clinical symptoms start with an itching sensation, which is followed by the development of a rash or petechiae, and in many hypersensitive persons papular eruptions appear together with intensive itching and edema. It is a self-limiting ailment if no further infection is contracted. It is neither a communicable disease nor a fatal one, but the discomfort and the pathology of the infection contribute to its importance in the field of public health and veterinary medicine.

The disease is of geographical interest because it is a "Disease of the Place," as explained by Jarcho and Van Burkalow (1952). Normally the adults of the dermatitis-producing schistosomes are blood parasites of birds, or, in some instances, of mammals. The life cycle begins with the hatching of the eggs which are present in the droppings of infected animals. Suitable species of snails become infected upon contact with the miracidia hatched from the eggs, the snails serving as the intermediate host. After a proper incubation period in the snail, the infectious schistosome cercariae are issued into the surrounding water. Upon exposure to these cercariae, the bird or mammalian definitive hosts are infected and the parasites mature in the vascular system of the hosts. The life cycle is completed when the adult worms produce eggs. Humans contracting the cercarial dermatitis are only the result of accidental intrusion into the life cycle of these interesting parasites.

Therefore in any geographical area, the conditions responsible for the occurrence of cercarial dermatitis are: (1) the presence of birds infected with dermatitis-producing schistosomes, (2) the presence of the snail intermediate hosts with habits conducive to the acquisition of the disease, (3) ecological conditions favorable for the survival of both the hosts and the parasites, and (4) the presence of human beings engaged in an activity which exposes them to the infection. In many parts of the world these four basic factors are present, and, as a result, the distribution of cercarial dermatitis is worldwide (Cort, 1950; Kuntz, 1955).

In the Pacific area, the disease occurs at various locations on the west coast of the North American continent extending north to Alaska. It has been reported from Japan, the Federation of Malaya, Australia, and as far south as New Zealand. The Hawaiian Islands chain is not entirely free from the presence of this disease. The following report is an attempt to summarize from the literature[3] the important facts concerning the vectors and reservoir hosts of cercarial dermatitis and to emphasize the distribution and transmission of both fresh-water and marine schistosomes in various parts of the Pacific.

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[3] The survey of literature on cercarial dermatitis was concluded in July, 1957.

quiries on cercarial dermatitis: Dr. W. R. Giedt, chief of Division of Epidemiology and Laboratories, Department of Health, Washington; Richard F. Peters, chief of Bureau of Vector Control, and Benjamin Keh, assistant vector control specialist, Bureau of Vector Control, Department of Public Health, California; Ralph B. Williams, director of Division of Public Health Laboratories, Alaskan Department of Health; Curtiss M. Everets, Jr., director of Division of Sanitation and Engineering, Oregon State Board of Health; Dr. W. E. Martin, professor of zoology and chairman, Department of Biology, University of Southern California; and Dr. H. F. Hsu, research assistant professor, Department of Hygiene and Preventive Medicine, State University of Iowa. Special thanks are offered Dr. J. R. Audy, of the Institute for Medical Research, Kuala Lumpur, Federation of Malaya, for suggesting the preparation of this report and for the invitation to participate in this symposium, General Ecology of Man, Animal Reservoirs, and Vectors in Relation to Disease, at the Ninth Pacific Science Congress.

A. FRESH-WATER CERCARIAL DERMATITIS

1. *United States and Canadian Pacific Coasts*

The etiology of swimmer's itch was first elucidated by Cort in Michigan, U. S. A., in 1928. Since that time, it has been recognized that "nonhuman" species of schistosomes are responsible for many cases of swimmer's itch. In the United States and Canada, Jarcho and Van Burkalow (1952) indicated recently in their report that "the states most strongly affected are Michigan, Wisconsin, and Minnesota. A few clinical cases (cercariae not identified) have been reported from the neighboring states of Indiana, Illinois, Iowa, Nebraska, and North and South Dakota. In Canada the major areas are in Ontario, east of Georgian Bay; in Manitoba, in and near Lake Winnipeg; in Saskatchewan; and in Alberta." Other areas mentioned in the text include: British Columbia, Washington, Oregon, Quebec, New York, Maine, Nevada, Oklahoma, Alabama, Tennessee, and Florida. The disease is common in lakes and swamps along the flyways of migratory water fowls.

Recent data, together with previous reports relative to the following Pacific states, are given as follows:

a. *Washington.* Miller (1925, 1927) was first to describe the presence of schistosome cercariae in the northwestern United States. *Cercaria elvae* from *Lymnaea stagnalis* Linn. and *Cercaria tuckerensis* from *Planorbis* spp. were obtained from Trout Lake, San Juan Sound, Washington. Swimmer's itch in the Seattle area was shown by Hunter, Shillam, Trott, and Howell (1949) to be caused by two agents: (1) the cercariae of *Trichobilharzia ocellata* (La Valette) (=*C. elvae*) from *Stagnicola palustris nutaliana*, and (2) *Cercaria physellae* of *T. physellae* (Talbot) from *Physella propinqua* (Tryon). The former species of snail was found associated with reeds and other aquatic vegetation growing in the gravel and mud bottom of the lake. It was thought that the cercariae from infected snails were carried to shore by currents created by the wind blowing towards the beaches. A similar situation was known to have existed in Douglas Lake, Michigan (Cort, 1936).

The definitive hosts for these parasites in Washington have not been described, but, according to McMullen and Beaver (1945), *C. physellae*, whose definitive host was reported to be the blue-winged teal, *Querquedula discors* (Linn.), was also infective to pigeons, mallards, and canaries; however, a Caspian tern, chickens, domestic ducklings, and gulls could not be infected. The blue-winged teal is also the definitive host of *T. ocellata* (=*T. Kossarewi*), but McMullen and Beaver showed that canaries, domestic ducklings, mallards, and pigeons could be the experimental hosts. (Chicks and a tern were resistant.) Recently Farr and Blankemeyer (1956) described a new species of schistosome, *Trichobilharzia brantae*, whose definitive host was a Canada goose (*Branta canadensis* L.) from the Turnbull National Wildlife Refuge, Washington.

Macy (1952) demonstrated that *C. elvae* from *Lymnaea stagnalis* was the causative agent for dermatitis cases at Cascade Lake, Orcas Island. Macy (1955) further reported that dermatitis cases were found at a lake south of Tacoma, Washington, and from Lake Chelan and Goose Lake, Okanogan County, in eastern Washington. In spite of the fact that a large number of lakes in the state of Washington might have harbored schistosome-infected snails, Dr. W. R. Giedt, chief of Division of Epidemiology and Laboratories of the Department of Health, received only ten reports of cases in 1955 and ten during 1956 (personal communication, 1957). Since swimmer's itch is not a reportable disease, these statistics are probably incomplete. However, the preventive measures advocated by the health officers of Washington with regard to control and avoidance of the infection must have been successful, as is indicated by the low incidence of infections.

b. *Oregon*. Macy (1955) investigated schistosome dermatitis cases in the Blue Lake area near Troutdale, Oregon. The causative agent, *C. oregonensis* from *Physa ampularia*, was a schistosome species originally described by Macfarlane and Macy (1946). It is interesting to note that these infected snails occurred most abundantly on dead or decaying vegetation in lakes, ponds, and marshes. They laid their eggs in late summer and the next generation of snails matured enough to lay their eggs during the early spring. Snails infected during late summer could carry the schistosome through the winter; thus in the following spring and summer, infected snails of both the old and new generations might produce cercariae for a longer time and therefore possibly might cause a higher level of infection in humans.

c. *California*. Simmons, Martin, and Wagner (1951) reported that the first case of freshwater cercarial dermatitis in California was derived from an artificial lake at Alendra Park in Los Angeles County. Schistosome cercariae of three different types were obtained from *Physa osculans* (Haldeman) found in this lake. The taxonomic consideration of these cercariae is currently delayed because of the efficient control of the intermediate hosts by health officers (personal communication from Dr. W. E. Martin, 1957). Walker (1954) investigated a suspected outbreak of schistosome dermatitis at Twain Harte Lake, Tuolumne County, and found bifurcated cercariae coming from a mixture of *Physella* and *Lymnaea* snails. Taxonomic determinations of the schistosomes involved in these dermatitis cases are yet to be announced. Keh and Grodhaus (1957) reported swimmer's itch at a duck club in Yuba County. Cercariae of the "*ocellata*" group were obtained from *Physa* snails and later proven by experimental infection to belong to the *Trichobilharzia* group of bird schistosomes. As yet, there is no report of schistosome infected snails or cases of cercarial dermatitis in northern California.

d. *Canada*. As indicated previously, migratory water fowls such as the blue-winged teals are known to be the definitive hosts of dermatitis-producing schistosomes. Because of the many glaciated lakes and swamps which act as bird refuges, cercarial dermatitis in Canada is known to occur in many areas. Along the Pacific coast of Canada, only two species of dermatitis-producing schistosome cercariae have been reported. These cercariae were believed to be the agents responsible for a severe outbreak in 1950 at Cultus Lake, B. C. Edwards and Jansch (1955) described these two species as *Cercaria adamsi* and *C. columbiensis*, which have *Physa coniformis* Tryon as the intermediate host. The adult forms of *C. adamsi* are now designated as *Trichobilharzia adamsi* Edwards and Jansch, 1955. The definitive hosts for *C. adamsi* were believed to be wild water fowl because domestic ducks could be infected experimentally. The authors suggested that the close resemblance of *C. columbiensis* to the cercariae of *Gigantobilharzia huronensis* Najim would indicate that the pas-

seriform birds might be the natural definitive hosts for *C. columbiensis*. Goldfinches and cardinals are known to be the hosts for *G. huronensis*.

2. *Alaska*

Students interested in cercarial dermatitis have long suspected that the disease may be present in Alaska because this region is the home of many migratory water fowls (Gabrielson, 1952). Harkema (1953, 1954, 1955, 1957) reported in a series of papers that swimmer's itch occurred in the Fairbanks and Yukon Flat areas in the Alaskan interior. He made a study of the life history of one of the two schistosome cercariae obtained from infected snails in this area. A total of 80 bodies of water was investigated during the summers of 1952 and 1953, and 20 of these 80 harbored infected snails of the species *Lymnaea palustris*, *L. stagnalis*, and *L. auricularia*. The incidence of the infection in snails seemed to vary according to location and time of the year. Additional localities having infected snails were reported in 1957.

There were no extensive human infections derived from avian schistosomes in Alaska. Some cercarial dermatitis cases were observed in the Fairbanks area in the vicinity of Fort Yukon. Harkema (1957) used cercariae from the naturally infected *Lymnaea stagnalis* for experimental infections of ducklings, and the adult worm was identified as *Trichobilharzia alaskensis* Harkema, McKeever, and Becker. The other type of schistosome cercaria remains unidentified. However, two naturally infected baldpate ducks harbored adult schistosomes belonging to the genus *Trichobilharzia*. So far there has not been an extensive study of the bird definitive hosts for schistosomes in Alaska.

Gabrielson (1952), in discussing Alaskan waterfowls and their management, stated that "Alaska has breeding populations of the Whistling Swan, Emperor Goose, White-cheeked Goose, Lesser Canada Goose, Cackling Goose, White-fronted Goose, and Black Brant. It also provides suitable nesting habitats for impressive numbers of Pintails, Mallards, Green-winged Teals, Baldpates, and Shovelers, among shallow water ducks." He thinks that the Yukon delta is not only the most important breeding area in Alaska, but one of the great waterfowl production units of the continent. The green-winged teals, pintails, and baldpates, which have an extensive continental breeding range, are less affected by man-made changes in Alaskan topography than are the other species of waterfowls. Therefore in the future, the baldpates, green-winged teals, and pintails are more likely to be implicated as reservoir hosts for the distribution of avian schistosomes.

3. *Mexico and El Salvador*

Possible fresh-water cercarial dermatitis from Lake Texcoco near Mexico City was reported by Cort (1950), but so far is unconfirmed. As far as this reviewer is aware, the only cases of swimmer's itch south of Mexico along the Pacific were those contracted from Lake Coatepeque, El Salvador, and reported by Reyes in 1944. According to Cort's account of the investigation by Reyes, the exact etiological agent was not identified. Jarcho and Van Burkalow (1952) reported that a blue-winged teal captured in this area had migrated from Douglas Lake, Michigan—the area where Professor W. W. Cort first found the cause of swimmer's itch. These blue-winged teals, according to these authors, migrate along the Mississippi River and the Atlantic coast flyways. The wintering grounds involved a large geographical area ranging from southern Florida, Texas, California, through Central America to parts of the northern South American continent, while the breeding grounds extend from the Great Lakes region westward to the Rockies and as far north as northwestern Canada.

Gabrielson (1952) showed that certain species of migratory fowls did migrate as far south as Mexico and that they could be recovered in British Columbia and the states of

Washington, Oregon, and California. Thus it is no surprise that swimmer's itch along the Pacific coast has been reported from Alaska to El Salvador.

4. *Japan*

On the western side of the Pacific Ocean, the Japanese have recognised for over 50 years the existence of a dermatitis of unknown etiology which occurred among farmers inhabiting land near Lake Shinji, Shimane Prefecture. The dermatitis is called "koganbyo" or "lakeside disease" (Hunter, Ritchie, and Tanabe, 1951).

These authors reported that Tanabe in 1947 was able to produce experimental dermatitis using the furcocercous cercariae from a species of snail now known as *Polypylis hemisphaerula* Benson. This observation was confirmed and subsequently the definitive hosts were determined. They are the large starling (*Spodiopsar cineraceus* Tamminck), the sparrow (*Passer montanus saturatus* Stejnerger), and the wagtail (*Motacilla* (*Motacilla*) *grandis* Sharpe). The adult of this species of schistosome is designated as *Gigantobilharzia sturniae* Tanabe, 1948.

The snail intermediate hosts (with 3–10 per cent infections) were commonly found on submerged vegetation or mud of rice fields and irrigation canals. Dermatitis began in mid-May and reached a peak about mid-July to mid-August, and the degree and intensity of the infection appeared to be correlated with the aquatic activity of the rice farmers. Surveys made of other areas in Japan indicated that both the bird definitive hosts and the snail intermediate hosts were widespread. Aside from Lake Shinji, the cases of dermatitis in the farmers of Mie Prefecture as well as those of Aichi Prefecture were believed to be caused by the cercariae of *G. sturniae* (Oda, 1956*a*, 1956*b*). It is possible that there are other areas in Japan where koganbyo exists.

Yamaguti (1941) reported the presence of avian schistosomes in Japanese birds and described two new species: *Trichobilharzia corvi* (Yamaguti, 1941) McMullen and Beaver, 1945, from *Corvus corone corone* Linn., and *Ornithobilharzia emberizae* Yamaguti, 1941, from *Emberiza sulphurata* Temm. et Schleg. However, it is not known if these parasites are capable of producing cercarial dermatitis.

An interesting report was made by Ito (1956) on a brackish water furcocercous cercaria from a snail intermediate host, *Tympanotonus microptera* (Kiener) found in Chiba Prefecture (Tokyo Bay). The author named it *Cercaria tympanotoni* and suggested that on morphological grounds this cercaria might be dermatitis producing. Because of an insufficiency of snails infected with this parasite, no experimental data were obtained. However, this record indicates, for the first time in Japan, that perhaps in a brackish water environment there is a possibility of humans contracting cercarial dermatitis.

5. *China and Formosa*

There are no reported cases in man of avian cercarial dermatitis in China or Formosa. However, two species of bird schistosomes have been found in China; *Ornithobilharzia odhneri* Faust, 1924, from the Asiatic curlew, and *Ornithobilharzia hoepplii* Tang, 1951, from Swinhoe's snipe.

In Formosa, one species of avian schistosome, *Trichobilharzia yokogawai* (Oiso, 1927) McMullen and Beaver, 1945, has been isolated from the duck. The "nonhuman zoophilic" strain of *Schistosoma japonicum* in Formosa has been regarded as a dog strain, because there is a high incidence (62 per cent) of natural infections in dogs but no known occurrence in humans (Hsu *et al.*, 1954). In order to determine the effectiveness of this strain in causing cercarial dermatitis and other symptoms in man, Hsu and Hsu (1956) tested the infectivity of this strain of *S. japonicum* on five human volunteers. The cercariae of *S. japonicum* did cause the sensation of itching and the development of a rash or papule. There were systemic clinical signs, such as abdominal pain, headache, nausea,

anorexia, chest pain, and general malaise, which are normally absent from avian schistosome cercarial infection. Nevertheless, the Formosan strain of *S. japonicum* did not develop to maturity in the volunteers and consequently did not result in a typical schistosomiasis. There were no experiments on repeated infections in these volunteers to determine hypersensitivity reactions.

Japanese investigators had long suspected that *S. japonicum* ("human strain") might cause cercarial dermatitis. In 1909, Kobayashi studied the relations between "kabure," endemic dermatitis, and schistosomiasis japonica (Faust, 1924*b*). Recently Ishii and Ogawa (1952) reported that it was possible to produce dermatitis in rats with the cercariae of *S. japonicum* ("human strain") by repeated exposure to the cercariae. Characteristic lesions included macules, papules, erythema, edema, and vesicles. However, Hunter and his associates (1956), using mice, hamsters, and rabbits as experimental animals, were unable to repeat these results or similar findings reported by other workers and so concluded that the selection of the proper experimental hosts for studies on immunologic responses to schistosome infection is of critical importance.

6. *Malaya and the Philippines*

Buckley (1928) demonstrated that the dermatitis known as "sawah itch" in Malaya was caused by the cercariae of *Schistosoma spindale* Montgomery, 1906, obtained from *Planorbis pfeifferi*. Normally *S. spindale* causes serious schistosomiasis in mammals such as cattle, sheep, goats, horses, antelopes, and water buffaloes in India, South Africa, and Sumatra.

Another example of a mammal-infecting schistosome which causes dermatitis in man is *Schistosomatium douthitti* (Cort, 1914). This organism is found in the United States as a parasite in deer, mice, and muskrats.

A fruitful field for research would be a comparative study to determine the differences between the mammalian schistosomes, which can cause dermatitis in man (like *S. spindale*, *S. douthitti*), and the dog-infecting strain of schistosome (*S. japonicum*), which apparently does not cause natural cercarial dermatitis (koganbyo) among Formosan farmers.

Recently a bird schistosome belonging to the "*elvae*" group of cercariae was described by Sandosham (1953) as the cause of sawah itch in the Ayer-Lunging district, Negri Semilan, and the intermediate host was identified as *Lymnaea rosseana* Mabille. This dermatitis-producing cercaria was named *Cercaria Malaya I*, and an unsuccessful attempt was made to infect chickens with it.

Cercarial dermatitis in man in the Philippines has not been studied to any extent, probably because of the intense efforts on the part of the medical scientists to control the spread of schistosomiasis japonica. Tubangui (1947) listed *Austrobilharzia hayensis* Tubangui, 1933, as a schistosome from the mesenteric vein of a snipe, *Capella gallinago gallinago*. This finding is encouraging for those who are interested in further host examinations for the presence of avian schistosomiasis, especially in the sea and shore birds of the Philippines.

7. *New Zealand*

According to Macfarlane (1944, 1949*a*, 1949*b*) the reports of swimmer's itch derived from lakes Hawea, Te Anau, Alexandrina, and Rotoiti, and from several lakes in the Rotorua district, have not been confirmed. However, Macfarlane recovered schistosome cercariae from snails in lakes Wanaka, Hayes, and Wakatipu in the South Island. The etiological agent causing experimental dermatitis has been described and named *Cercaria longicauda* Macfarlane, 1944. The snail intermediate hosts are: *Myxas ampulla*, *M. arguta*, and *Limnaea alfredi*. The molluscan hosts in Lake Wanaka lived in beds of the pond weed *Myriophyllum robustum* and also on *Isoetes* spp., *Juncus* spp., and *Potamogeton polygonifolium*. In lakes Wakatipu and Hayes there were

fewer snails, associated with the weed *Ranunculus fluitans*. The definitive host, the teal *Fuligula novae zealandii*, rested on the weed beds through the summer and fed on the lake floor. The adult stage of *C. longicauda* has not been studied.

8. *Australia*

Fresh-water cercarial dermatitis has been known in Australia since Johnston (1941) first reported its presence in the Murray Valley swamps. He surmised that *Cercaria parocellata* Johnston and Simpson, 1939, from *Limnaea lessoni*, on morphological grounds, might be the parasite involved. Macfarlane (1952) made a further investigation and obtained reports of dermatitis at Albury, Birri, Loxton, Mannum, Murray Bridge, and Tailem Bend near Adelaide. According to this author, at all of these places the river spread into areas of shallow water, which allowed the molluscan hosts to build up a population in close association with water birds. He believed that most of the infection of humans occurred during periods of shallow water.

Swimmer's itch was also known to be present in Western Australia. Lake Bumbleyung in the Wagin region appeared to be the important area although other smaller lakes had also been the source of the infection. The third area in Australia suspected to have cercarial dermatitis was Narrabeen Lake, a small shallow coastal lake near Sidney. It has been reported since that these cases were caused by marine species of bird schistosomes, because this lake has an outlet to the Pacific Ocean and the water may not be fresh.

Macfarlane reported that the snail intermediate host *L. lessoni* occurred in both the Murray Swamp area and the Wagin region. Whether or not *Cercaria paracellata* was involved in both areas is not known. In the Murray River, *L. lessoni* lived in the often stagnant backwaters.

Johnston (1941) suspected that the black swan was the definitive host for *C. parocellata*, but confirmation has not been made. *Cercaria jaenschi* was reported by Macfarlane (1952) not to penetrate the skin of man even though it was a schistosome cercaria. Furthermore, the antigen prepared from these cercariae produced smaller and less persistent skin reactions than did the *C. parocellata* antigen.

B. MARINE CERCARIAL DERMATITIS

1. *California and Mexico*

Extended studies of marine snails as possible agents in the transmission of cercarial dermatitis were not made until several years after World War II. However, as early as 1942, Penner mentioned that the marine gastropods might be infected with dermatitis-producing schistosome cercariae. In 1950, he described as a new species *Cercaria littorinalinae* from the marine snail *Littorina planaxis* Philippi, which were collected along the rocky shores of the Coronado Islands in Mexico and from Bird Rock near La Jolla, California. The natural definitive host was the Wyman western gull (*Larus occidentalis wymani* Dicky and van Rossem). Penner (1953c) was able to infect experimentally with this species of cercaria the following birds: brant, cormorant, black-crowned night heron, western gull, budgerigar parakeet, Australian zebra finch, domestic pigeon, red jungle fowl, and linnet. The domestic duck did not appear to be susceptible to the infection. The adults of *C. littorinalinae* belong to the genus *Austrobilharzia* (Johnston, 1917) and have been given the name *Austrobilharzia littorinalinae* by Penner although the taxonomic description is still unavailable. This species of schistosome is therefore distinct from *A. variglandis* (Miller and Northup, 1926) Penner, 1953 (= *Microbilharzia variglandis* (Miller and Northup, 1926) Stunkard and Hinchliffe, 1951).

In the San Diego area, this marine species of bird schistosome has not been officially incriminated in cases of swimmer's itch although Penner (1950) did mention that he experienced the development of typical lesions after wading in sea water in this area

while collecting the snail intermediate hosts. Cercarial dermatitis can be produced experimentally with *C. littorinalinae*.

Recently Gradhaus and Keh (unpublished data, 1957) reported cases of swimmer's itch occurring on the beaches of the city of Alameda, bordering San Francisco Bay. *Nassarius obsoletus*, a marine snail intermediate host for *A. variglandis* on the Atlantic coast, was also the intermediate host in California. It was believed that the snails were introduced into this area together with the oysters that had been planted in the bay. The schistosome cercariae from these snails were identified as those of *A. variglandis*.

2. *Hawaiian Islands*

Chu (1952) first reported the presence of a dermatitis-producing schistosome cercaria from the marine snail *Littorina pintado* Wood in two bird refuges on small offshore islands near Oahu, known as Bird Island (Moku Manu) and Rabbit Island (Manana). The snails infected with schistosomes were found only in the sea benches where there were many small tidal pools constantly receiving a sea spray. Collectors of the snails from the sea benches of Rabbit Island experienced itching and, in some cases, developed typical schistosome papule lesions on their feet. It may be added that the distribution of infectious cercariae seems to be limited to the bird refuges, because Chu and Cutress (unpublished data, 1954) were unable to find schistosome-infected snails inhabiting any of the swimming beaches on the major islands of Oahu, Maui, Kauai, and Hawaii. The life history of this parasite has been reported by Chu and Cutress (1954). The natural definitive host for the adult stage was the ruddy turnstone (*Arenaria interpres interpres*), a shore bird which winters in the Hawaiian Islands. Chicks, ducks, and the sooty and noddy terns could be infected experimentally.

After a study of the morphological characters of the adult stage of the schistosome in the naturally infected turnstones as well as in the experimentally infected animals, the authors concluded that this species was the same as the species of schistosome reported by Stunkard and Hinchliffe (1951, 1952) from the eastern United States along the Atlantic Ocean, i. e., *Austrobilharzia variglandis*.

Penner (1953*b*) reported that the red-breasted merganser (*Mergus serrator* L.) was the natural definitive host for *A. variglandis* in the Atlantic coast. Munro (1944) states that this species of bird had been reported only as an occasional visitor to the Hawaiian Islands. However, Richardson and Fisher (1950) do not list the red-breasted merganser as a species found in the Hawaiian bird refuges. It can also be added that the western gull, a natural definitive host for *A. littorinalinae* in California, is not a species generally seen on Oahu.

The migration routes for shore birds in the Pacific Ocean have been studied by Baker (1951). On the basis of sight records, specimen collection, known statistics of breeding and wintering, and from a study of maps of the region, he established the following three flyways: (1) the Asiatic-Palauan, (2) the Japanese-Marianan, and (3) the Nearctic-Hawaiian. For each of the flyways the author listed the names of the regularly visiting and the uncommonly visiting shore birds. Of the 35 species mentioned, only the ruddy turnstone and the golden plover (*Pluvialis dominica fulva*) were the ones common to all of the three flyways. In the experience of the Hawaiian investigators, the golden plover was never found to be infected with the schistosome, in contrast to the ruddy turnstone.

King (1955) listed six major groups of sea birds found in the central Pacific Ocean. These are: (1) the albatrosses, (2) the shearwaters and petrels, (3) the terns, (4) the frigate birds, (5) the boobies, and (6) the tropic birds. Gulls and jaegers were listed as being occasionally seen. Chu and Cutress (unpublished data, 1954) did not encounter a single case of natural infection with schistosomes in limited examinations of sea bird pop-

ulations. The exact relation of the sea birds to the problem of transmission and reservoir hosts in Hawaii has yet to be determined.

The snail intermediate host, *L. pintado*, uncommon in Micronesia and apparently limited in its range to the northern Pacific islands, has been reported by Demond (1957) to exist in southern Japan, the Ryukyus, Bonins, northern Philippines, Marianas, Marshalls[4], Johnston Island, and Formosa. The experimental snail intermediate host used by Chu and Cutress, *Littorina scabra* L., has a much wider geographical range: from east Africa through the Indian and Pacific oceans to Hawaii and Tahiti, and from the Ryukyus, the Philippines, and Marianas, south to northern Australia. Since both the definitive and intermediate hosts for *A. variglandis* are widely spread in the Pacific area, one may surmise that marine schistosome infections of birds and snails may not be limited to the Hawaiian Islands and California and that with further investigation other areas might prove to be infected.

In determining the casual agent of swimmer's itch, or cercarial dermatitis, it is not sufficient to find schistosome-infected snails in the area because of the possible presence of other etiological agents which cause similar skin lesions. "Swimmers' Itch" (or "Pearl Harbor Itch") cases reported by Arnold and Bonnet (1950) are now suspected to have been cases of marine hydroid dermatitis, because the discovery of a medusa (*Sarsia* sp.) was made in the same location which Arnold and Bonnet reported to be a source of the dermatitis. This finding, together with the absence of schistosome-infected snails in the areas under study, suggests that these "Swimmers' Itch" cases of Arnold and Bonnet were not of cercarial origin (Chu and Cutress, unpublished data).

It is necessary, however, to point out that in the Atlantic coast, (such as Mill cove in Maine, Narragansett Bay in Rhode Island, and Long Island Sound, N. Y.) cercarial dermatitis was reported to be associated with clam digging (Orris and Combs, 1950; Sindermann and Gibbs, 1953). The intermediate host is a mud snail, *Nassarius obsoletus* (*Nassa obsoleta*), which is also an intermediate host for the marine schistosome in California. This species is not found in Hawaii as Edmondson (1946) listed *Nassa sertum* Bruguiere as the only local species. In several surveys made during 1951–54 by the Hawaiian investigators, the few bottom-dwelling gastropods from West Loch, Pearl Harbor, were never found to be infected with schistosome parasites.

Demond (1957) listed *Nassarius papillosus* (Linn.) as occurring in Hawaii. As yet, there is no report indicating that this or any other species of *Nassarius* is an intermediate host for schistosome in the central and south Pacific.

An example of the difficulty of determining the etiological agent for dermatitis caused by marine microorganisms is that reported by Strauss (1956) for the "Seabather's Eruption" in Guantanamo Bay, Cuba. This investigator was unable to find any snails infected with schistosomes. Serological tests of the patients showed negative evidence for the presence of cercarial dermatitis. A more fortunate experience than that reported by Strauss was given by Chu and Cutress (1955). Many construction workers contracted dermatitis when in contact with sea water in Hilo Bay, Hawaii. Although in this area, *Littorina pintado* and the ruddy turnstone were seen, no schistosome-infected snails were located. Instead, a marine hydroid, *Syncoryne mirabilis* (Agassiz, 1852), was found growing profusely on the surface of the submerged rocks near the site of construction. By chemical treatment, the hydroids were destroyed and the dermatitis was controlled.

Most of the conclusions incriminating marine schistosome cercariae in cases of derma-

[4] In 1955, at Eniwetok, C. E. Cutress found *L. pintado* and ruddy turnstones in the area, but among the specimens examined by him no schistosomes were found (personal communication, 1957).

titis have been based upon circumstantial evidence. The urgent need in diagnosing the cause of naturally occurring dermatitis is a technic (e. g., biopsy tests) which would yield direct evidence about the infective agent, so that proper control methods could be formulated.

3. *Australia*

Bearup (1955, 1956) showed that schistosome cercariae occurred in a marine snail, *Pyrazus australis* Quoy and Gaimard, in Narrabeen Lake, near Sydney, N. S. W. The cercaria was first identified as *Cercaria variglandis* later Miller and Northup, subspecies *pyrazi*, but was determined to be the cercaria of *Austrobilharzia terrigalensis* Johnston, 1917. The seagulls (*Larus novae-hollandiae*) from the Sydney district were heavily infected.

The incidence of schistosome infection in *P. australis* from Narrabeen Lagoon was 4–6 per cent, the higher level occurring during the hot months at the end of the year. Cercariae from these infected snails would infect young seagulls, budgerigars (*Melopsitacus undulatus*), and pigeons (*Columba livia*), but not domestic ducks or mice.

From Florida, U. S. A., several marine schistosome cercariae have been described (Hutton, 1952; Leigh, 1955; Penner, 1953*a*). These species are distinct from one another and different from *A. variglandis*. However, the extreme similarity in morphology of the three species, namely, (1) *A. variglandis* from the Atlantic, Pacific, and Hawaiian areas, (2) *A. littorinalinae* from southern California and Mexico, and (3) *A. terrigalensis* from Australia, raises the interesting question of whether or not they are actually one species with minor variations because of adaptation to the intermediate and definitive hosts in widely separated geographical areas.

DISCUSSION

Cercarial dermatitis is of worldwide distribution, and probably there are other areas where suspected cases of swimmer's itch occur but where no investigations have been made. In the Pacific Ocean area, many islands in the Polynesian, Micronesian, and Melanesian groups are worthy of exploratory studies for the presence of bird schistosomiasis. Likewise, other geographical areas such as China, Formosa, Indonesia, Viet Nam, the Philippines, and Thailand have yet to be investigated fully.

In the North American continent, swimmer's itch has been widely studied, yet data on schistosome infections in migratory birds are still limited. Most of the information on definitive hosts has been obtained through experimental infection. As a result, the question is frequently asked as to the degree of natural infection with schistosomes in other types of birds. In this connection, the problem of host susceptibility has been studied by many investigators. In our own experience, the marine schistosome adults found in the ruddy turnstone developed well in the sooty and noddy terns, but in chicks and ducks the adults did not remain viable for an extended period and the pathology was not entirely comparable to that in the natural host. This differential susceptibility between species and subspecies (or strains) of the birds is a challenging problem to workers who are interested in immunology. Such a study is important in relationship to speciation and distribution of both the fresh-water and marine schistosomes in birds.

Specificity of a trematode parasite for a host may be directly correlated with the host diet. An example of this correlation was reported by Oguri and Chu (1955) for the infection of domestic ducks by the cloacal trematode *Parochis acanthus* (Nicoll, 1906) Nicoll, 1907. The natural definitive hosts for this parasite are sea birds. When the infectious cysts of *P. acanthus* were given orally to mash-fed ducks, there were no infections in these experimental hosts. However, if the ducks were fed with squids from the sea, instead of the mash diet, it was possible to establish the

infection in them. This variation in host susceptibility caused by a change in diet suggests that seemingly contradictory results from host experimental infections for bird schistosomes may be due to differences in the diets fed the experimental hosts by the various investigators.

Substantial data, on the other hand, have accumulated during the past several decades regarding the bionomics of the intermediate hosts of the dermatitis-producing schistosomes. These data are chiefly concerned with (1) the habits of the snails, such as their food requirements, reproductive rates, adaptation to surroundings, and association with other plant and animal life, (2) the environmental conditions such as changes in pH and salinity in water, variation in temperature and amount of sunlight, and (3) susceptibility of the other species of snails in the locality to infection by the schistosome miracidia. This information is essential for understanding the reasons why the disease exists in specific localities. Many reports also indicate that an intimate association between the infected birds and the snail intermediate hosts is a necessity before cercarial dermatitis can be established as a "Disease of the Place."

For fresh-water snails, cultivation in the laboratory has not been a problem, but for marine snails, technics for their cultivation are yet to be developed. The bionomics of marine snails is a fascinating subject. Edmondson (1946) stated that: "A specimen of *Littorina pintado* remained attached to the plastered wall of the Marine Biological Laboratory, Honolulu, for nearly a year. When it was returned to sea water it regained its activity in a few minutes." Attempts are now being made to breed *Littorina* snails in our laboratory for use in experimental work on schistosomes.

The investigation of all phases concerned with marine cercarial dermatitis is indeed a green pasture for those who are interested in diseases associated with a marine environment. We encourage investigators in the Pacific area to participate in this field of study.

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Some Observations on the Lagoon Plankton of Eniwetok Atoll[1]

MALVERN GILMARTIN[2]

DURING THE COURSE OF a translagoon ecological study conducted in the northern Marshall Islands during 1955, a series of plankton hauls were taken. Subsequent analysis revealed several interesting aspects of lagoon plankton, in addition to recording the forms present.

Eniwetok Atoll lies at about 11° 30′ N. latitude and 162° 15′ W. longitude. The atoll is composed of 38 islets on a reef surrounding an oval lagoon approximately 30 kilometers wide and 40 kilometers long. The lagoon is essentially a self-contained body of water with a maximum depth of 65 meters. There are 3 major passes between the lagoon and the open ocean; southeast pass, 550 meters wide with an average depth of 31 meters, south pass, 9.5 kilometers wide with an average depth of 18 meters, and southwest pass, 4.3 kilometers wide with an average depth of 7 meters.

From 4 April 1955 to 29 December 1955, 21 plankton hauls were made along a transect extending from between Giriinien and Rigili islets to Aniyaanii Islet (Fig. 1). Each individual series contained a haul made just inside the reef on the east end of the transect, from 1 to 3 hauls equidistantly placed along the transect, and a haul taken just inside the reef on the west end of the transect. All series were completed during periods within 2½ hours of local apparent noon. Individual series were taken at speeds from 1 to 2½ knots at depths ranging from 1 to 3 meters. The plankton collected were stored in 10 per cent sea water–formalin for subsequent treatment. All hauls were taken using a one-half meter plankton net constructed for quantitative work (Tester, 1955) with an internally mounted Atlas-style flow meter.

During this period, standard oceanographic observations were made. The mean value, range, and standard deviation of certain physical and chemical characteristics of the transect surface water is indicated below.

	Temperature °C.	Salinity ‰	Oxygen % sat.
mean	28.61	34.37	90.0
range	28.31–29.13	34.05–34.67	59.9–104.7
σ	.023	.046	7.9

No apparent correlation was noted between these factors and the intralagoon plankton distribution.

The results of the plankton hauls, as indicated for occurrence in Table 1, for dominance in Figure 2, and for volume in Figure 3, suggest a surprisingly "endemic" (as opposed to

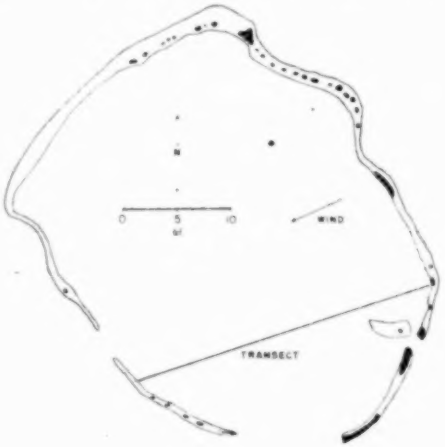

FIG. 1. Eniwetok Atoll showing transect line.

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TABLE 1

ABUNDANCE OF PLANKTON CONSTITUENTS BY HAUL
A = abundant, 5 per cent or more by number; C = common, 1–5 per cent by number;
S = scarce, less than 1 per cent by number

	PLANKTON HAUL AND DATE																				
	April 4				Nov. 10					Nov. 13			Dec. 26				Dec. 29				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Cyanophyta:																					
Trichodesmium erythraeum				S					S		S	S									
Chrysophyta:																					
Coscinodiscus sp.						C							S				C	C	C	S	
Protozoa:																					
Foraminifera sp.						S	S	S	S	S				S	S	S		S	S		S
Radiolaria sp.								S			S			S	A		S	S			
Coelenterata:																					
Anthozoa sp. (sea anemone)																	S				
Scyphozoa sp.	S	A	S	A	S	A	A	A	S	A	A	C	S	S		A					S
Siphonophora sp.	S		S	A	S				S			C			C	C	C		C	C	C
Ctenophora:	S	A	A														S				
Brachiopoda:																					
Lingula sp. larva	S	S	S		S	S									S						
Echinodermata:																					
Ophiuroidea sp. larva								C				S									
young adult																S					
Echinoidea sp. larva									S												
Chaetognatha:																					
Sagitta sp.	S																		C		
Sagitta enflata	A	A	A	A	A	A	A	A	A	C	A	C	A	A	A	S	C	C	C	C	C
Sagitta neglecta	S				S	A														C	S
Sagitta regularis					S				S											C	S
Mollusca:																					
Heteropoda																					
sp. larva																	S				
Atlanta sp.		S				S	S	S	S		S	S			S				S		A
Pteropoda																					
sp.																					
Creseis virgula								S			C	S									
Gastropoda																					
sp. larva			S		S	S	S	S	S	S		S		S	S		S	S	S		
Natica sp. larva		S				S					S	S									
Annelida:																					
sp. larva		S			S	S		S		S								S			
Arthropoda:																					
Copepoda sp.			S				S	S	S								S				
Arcartia sp.																		S			
Candacia ethiopica											S						S	S	S	S	
Centropages calanius											S						S		S	S	S
Copilia mirabilis										S											
Corycaeus sp.											S							S		S	
Euchaeta marina				S														S			
Labidocera sp.			S		S																
Labidocera laevidentata										S											
Macrosetella gracilis															S						
Neocalanus gracilis									S												
Oncaea sp.										S											
Arthropoda:																					
Pontellina plumata					S							S						S			
Pontellopsis sp.										S		S							S		

TABLE 1 (Continued)

ABUNDANCE OF PLANKTON CONSTITUENTS BY HAUL
A = abundant, 5 per cent or more by number; C = common, 1–5 per cent by number;
S = scarce, less than 1 per cent by number

	PLANKTON HAUL AND DATE																				
	April 4				Nov. 10					Nov. 13			Dec. 26				Dec. 29				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Sapphirina sp.		S									S	S								S	
Scolecithrix danae											S										
Tortanus gracilis					S																
Undinula vulgaris	C		S		S					S	S		C	C	S	S	O	C	S	S	
Amphipoda sp.	S	S		S		S	S			S	S	S		S							
Isopoda sp.										S											
Mysidacea sp.																	S				
Euphausiacea sp.									S	S		S			S					S	
Stomatopoda sp. larva		S		S	S	S		S	S		S	S			S	S		S			
Decapoda																					
Macrura larva	S		S	S	S	S	S	S	S	S	S	S	C							S	S
Anomura larva									S		S		S	S							
Brachyura zoea		C	S	S	S	S	S	A	A	C	A	A	A	A	C	S	S	S	A	A	S
Chordata:																					
Oikopleura sp.	A	A	A		A	A	A		S				C	S	S	A	S	S	C	C	
Salpa sp.		S					S	S	S			S									
Thalia democratica																		S			
fish eggs	S	S	S	S	S	S	S	S	S	S		S	S	C	C	C	A	A	C	C	A
Goby eggs	S	S			S	S			S				A		C		C	C			A
fish larva	S		S	S	S	S	S	S	S	S	S	S	S	S	S				O		
Monocanthus sp. larva								S													

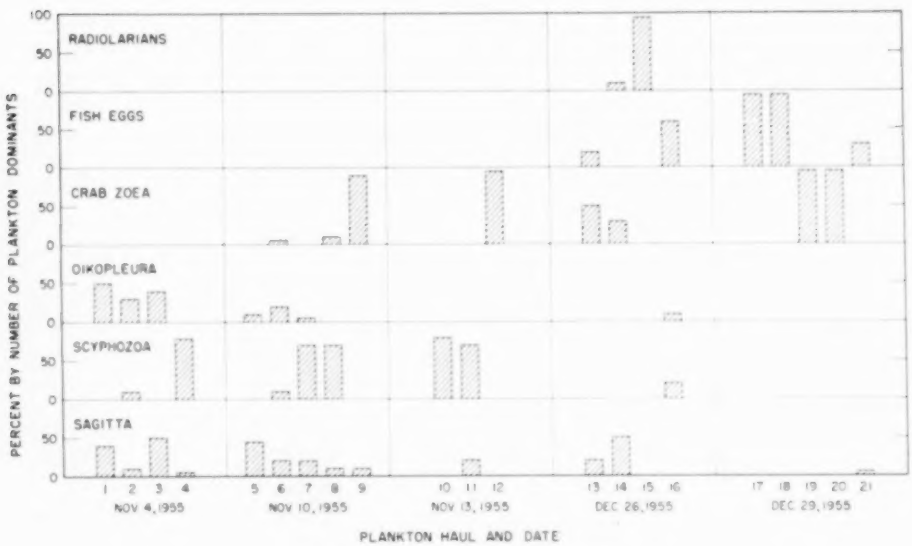

FIG. 2. Relative plankton constituents.

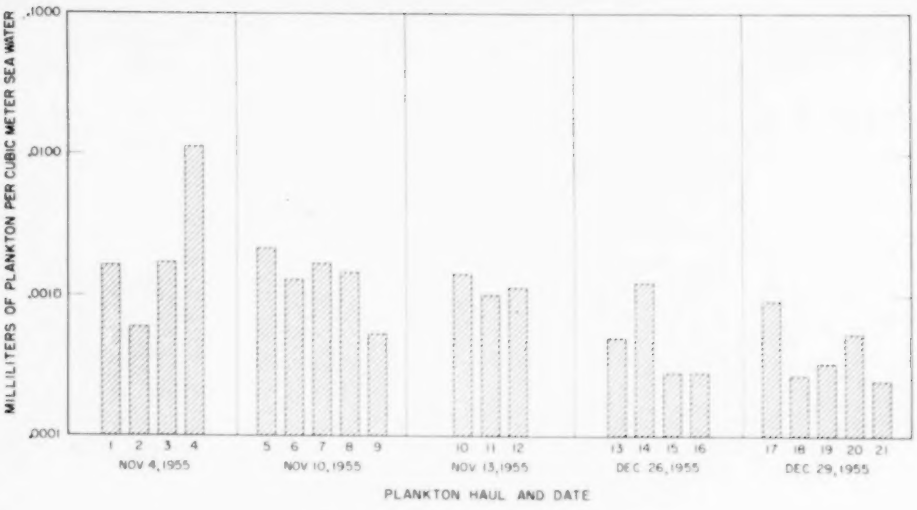

FIG. 3. Plankton settling volumes.

"transient") lagoon plankton population compared with that reported from other northern Marshall Islands atolls (Johnson, 1954). An analysis of the plankton dominants show that over half of the hauls were dominated by meroplanktonic forms, e.g., brachyura zoea, or groups the majority of which are neritic, e.g., scyphozoan medusea. In some of the hauls, these forms made up 95 per cent of the number of planktants collected. Certain of the species noted, e.g., *Undinula vulgaris*, have relatively long life cycles. For these and the noted meroplanktonic forms to maintain the relative concentrations indicated by these hauls would suggest a relatively stable body of lagoon water. The lack of numerous deep passes between the ocean and the lagoon, common in other northern Marshall Islands atolls, might explain this indicated restriction in water exchange.

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On Certain Thaliacea (Tunicata) from the Pacific Ocean, with Descriptions of Two New Species of Doliolids[1]

TAKASI TOKIOKA[2] and LEO BERNER[3]

THE MATERIAL upon which this paper is based has been taken from the extensive plankton collections available at the Scripps Institution of Oceanography. The samples examined were from three sources: the Shellback Expedition to the area off Central and South America in 1952, the Mid-Pacific Expedition to the Marshall Islands area in 1950, and from the routine Marine Life Research Program sampling off the west coast of the United States and Baja California, Mexico. The two expeditions were in part supported by grants from the Office of Naval Research. The Marine Life Research Program is the Scripps Institution's component of the California Cooperative Oceanic Fisheries Investigations, a project sponsored by the Marine Research Committee of California. The work has been further supported by a postdoctoral grant from the Rockefeller Foundation for the senior author.

Two new doliolids found in the plankton samples collected on the Shellback Expedition have already been described (Tokioka and Berner, 1957), and further examination of the samples has yielded two additional new doliolids from the same area.

In addition to the descriptions of the two new species, both of which belong to the genus *Doliolina*, additional notes are given on *Doliolina undulata* Tokioka and Berner 1957, *Doliopsoides horizoni* Tokioka and Berner 1957, *Doliolina intermedium* (Neumann) (1906), *Cyclosalpa strongylenteron* Berner 1955, and *Cyclosalpa bakeri* Ritter 1905.

Doliolina obscura new species
Fig. 1A–E

Many specimens of this species were found at Shellback stations 137, 142, 145, 155, 160, and 180. The species also occurs quite often in the samples collected by the Marine Life Research Program, although it is never numerous.

The gonozooids may be somewhat stumpy in outline; they are usually less than 5 mm. long and may range up to 4 mm. in body diameter. The test is of moderate thickness, is rather soft, and may be easily stripped from the body. When found with the test in place the specimens tend to be covered with detrital material from the sample.

Muscles I, VII, and VIII are narrower than muscles II-VI. Muscle VII is distinctly interrupted at the mid-ventral line. The sixth and seventh intermuscular zones, especially the latter, are narrower than the others.

The endostyle (*ed.*) is long, extending anteriorly at least to three-fourths of the second intermuscular zone and posteriorly to the anterior margin of muscle V. The anterior margin of the peripharyngeal band (*p.b.*) extends nearly to muscle I. The ciliated groove (*c.g.*) is situated in the middle of the second intermuscular zone. The dorsal ganglion (*d.g.*) is

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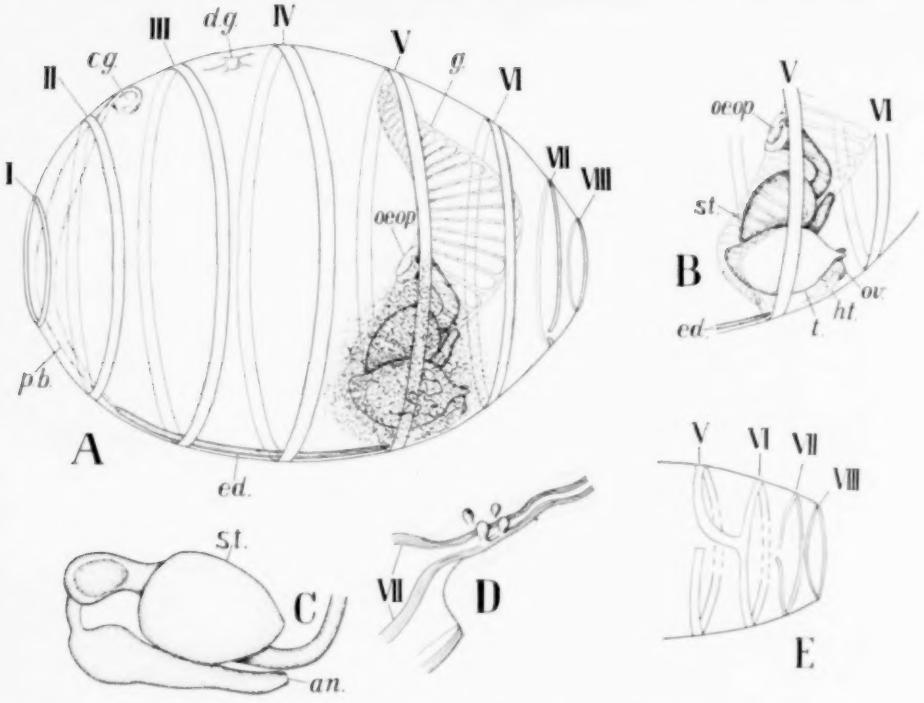

FIG. 1. *Doliolina obscura* n. sp. A, Animal from left side: a 5 mm. gonozooid. B, Alimentary organs and gonads from left side. C, Alimentary canal. D, Ventral protuberance, phorozooid. E, Aberrant form showing arrangement of muscles viewed ventrally.

Abbreviations: I-VIII, body muscles; *an.*, anus; *c.g.*, ciliated groove; *d.g.*, dorsal ganglion; *ed.*, endostyle; *g.*, gill septum; *ht.*, heart; *int.*, intestine; *oe.op.*, oesophageal opening; *ov.*, ovary; *pb.*, peripharyngeal band; *st.*, stomach; *t.*, testis; *v.d.*, vas deferens.

situated in the third intermuscular zone with its posterior edge at the center of the zone. The gill septum (*g.*) is sigmoid in shape extending from the dorsal to ventral position of muscle V, (Fig. 1*a*). At the lower flexure the anterior margin reaches slightly beyond the middle of the fourth intermuscular zone. At the upper flexure the posterior margin extends slightly beyond the posterior margin of muscle VI. The median crest of the gill septum is slightly displaced to the right side in the ventral half of its course, where the massive alimentary organs and gonads are situated. There are about 40 elongate stigmata.

The alimentary organs and gonads are surrounded by densely aggregated corpuscles which make it very difficult to examine the structure of the organs closely. These corpuscles are probably reddish orange when the animal is alive. Staining of the specimens with Rose Bengal makes it somewhat easier to study this portion of the body.

The oesophageal opening (*oe. op.*) is located near the center of the circle described by muscle V. The stomach (*st.*) is located on the sagittal plane of the body and is roughly oval in outline. The intestine forms a simple loop and ends with the anus (*an.*) at a posi-

tion slightly behind the cardiac end of the stomach. The hind stomach is distinct and there is an obvious constriction between it and the following portions of the gut.

The ovary (*ov.*) is located near the middle of the fifth intermuscular zone or slightly posterior to it. The testis (*t.*) is a fusiform-shaped stumpy mass, oriented anteroposteriorly, and extending from the ovary to near the middle of the fourth intermuscular zone. The heart is located near the ovary.

The phorozooid is similar in appearance to the gonozooid, though the corpuscular aggregation over the area of the gut tends to be reduced in the phorozooid. Both the ventral ends of muscle VII extend into the ventral protuberance (Fig. 1D).

At a glance this new species closely resembles *D. mülleri* (Krohn 1852). It differs from the latter by having the ventral interruption of muscle VII and in the anterior-posterior position of the testis. In *D. mülleri* the testis is situated somewhat dorsoventrally and muscle VII forms a complete loop. The sigmoid curve of the gill resembles *D. sigmoides* Garstang 1933 (= *Doliolum krohni* Neumann 1906). The new species completely lacks the epidermal tentaclelike processes characteristic of *D. sigmoides*. Interrupted muscle VII is another differentiating characteristic. The new species differs from *D. undulata* in the shape of the stomach and in the shape and location of the testis. In addition, the aggregation of corpuscles around the alimentary organs and the gonads is unique. The species name comes from this aggregation which makes these organs obscure.

The specimens upon which this description is in part based are deposited in the U.S. National Museum under the following numbers:

HOLOTYPE: U.S.N.M. no. 11371, *Doliolina obscura*, gonozooid, 1 specimen from Shellback station 137 located at 13° 43.5′ S. 81° 08.5′ W.

PARATYPES: U.S.N.M. no. 11372, gonozooids, 10 specimens, *Doliolina obscura* from Shellback station 137.

From the MLR material one aberrant form was taken in which the fifth body muscle was interrupted and the left limb of that muscle extended back to connect with muscle VI. In other respects this specimen did not differ from the species. The muscle arrangement is shown in Figure 1E.

Doliolina separata new species
Fig. 2

A few specimens of this diminutive doliolid were found in the samples from Shellback stations 137, 145, and 180. Most of them were poorly preserved and immature, but three mature, fairly well-preserved specimens were found at station 137. The following description is based on these three specimens.

The specimens were 1.5, 1.7, and 1.7 mm. long. The body is somewhat elongate. The test is of moderate thickness and is easily stripped from the body. Under the microscope many minute cells can be observed on the surface of the test.

Body muscles I, VII, and VIII are very narrow. Muscle II is somewhat narrower than muscles III-VI. Muscle VII is clearly interrupted at the mid-ventral line. The first and seventh intermuscular zones are narrower than the others.

The endostyle (*ed.*) is very long, extending from the posterior margin of muscle II to near the anterior margin of muscle V. The anterior border of the peripharyngeal band (*p.b.*) closely approaches muscle I. The ciliated groove (*c.g.*) is situated approximately in the middle of the second intermuscular zone. The dorsal ganglion (*d.g.*) is located in the third intermuscular zone near the posterior margin of muscle III. The gill septum (*g.*) extends from muscle VI dorsally to muscle V ventrally, and bears 10 pairs of somewhat elongate stigmata.

The oesophageal opening is located at the center of the circle formed by muscle VI. The whole alimentary canal forms an S-shaped loop towards the anteroventral side, in the

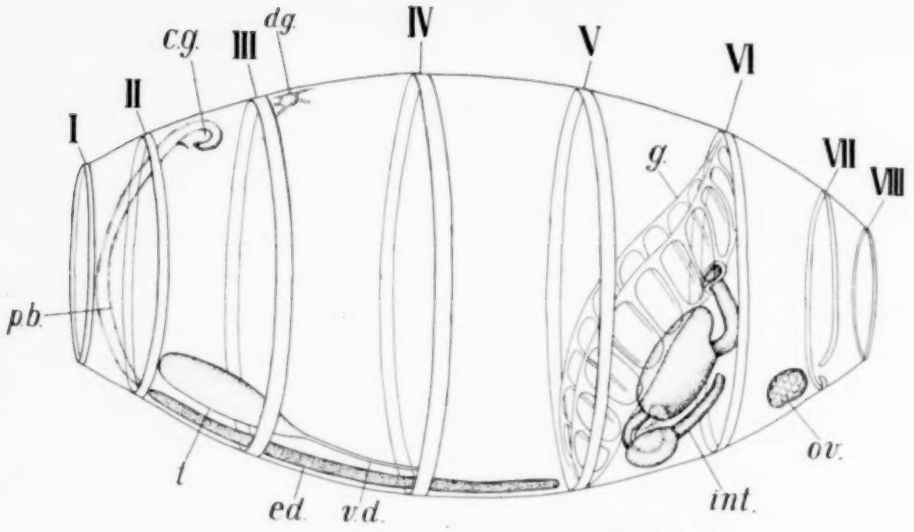

FIG. 2. *Doliolina separata* n. sp., a 1.7 mm. gonozooid from left side.

sagittal plane of the body. The stomach is roughly an elongate ellipse in outline with its cardiac portion prominently protruded. The anus opens near the cardiac end of the stomach. The anterior margin of the intestinal loop (*int.*) extends to near the posterior margin of muscle V. The mid-intestinal region is swollen in some specimens. Usually there is a small group of cells on each side of the intestinal loop, in some cases these groups may consist of two parts, one large and one small.

The ovary (*ov.*) is situated ventrally near the middle of the sixth intermuscular zone. The testis (*t.*) is a club-shaped organ extending from the posterior margin of muscle II to slightly beyond the posterior margin of muscle III. The vas deferens (*v.d.*) opens into the pharynx at the level of muscle IV.

The phorozooid is quite similar to the gonozooid. It lacks gonads and has a ventral protuberance, into which the ends of muscle VII project.

Doliolina separata n. sp. resembles *D. krohni* (Herdman 1888) and *D. indicum* (Neumann 1906) in that it has an obliquely stretched gill septum. The shape of the testis is somewhat reminiscent of *D. intermedium* (Neumann 1906). The ventral interruption of muscle VII and the peculiar arrangement of the gonads, in which the ovary and testis are widely separated from each other, is unique and this latter characteristic is the basis for the specific name here given.

The material upon which this description is in part based is deposited in the U.S. National Museum:

SYNTYPES: U.S.N.M. no. 11373, 2 specimens, Gonozooid, *Doliolina separata* from Shellback station 137.

ALLOTYPES: U.S.N.M. no. 11374, 4 specimens, Phorozooid, *Doliolina separata* from Shellback station 137.

Doliolina intermedia (Neumann 1906)
Fig. 3

Doliolum intermedium Neumann, 1906: 211–212.

Many specimens of *D. intermedium* have been found in the Shellback and the Mid-

Pacific material. They have an average length of about 10 mm. The test is very soft, of moderate thickness, and is easily stripped from the animal. All eight body muscles are complete. Muscles VII and VIII are very narrow and muscle VI is somewhat narrower than muscles I-V. The third intermuscular zone is the widest and the seventh is the narrowest.

The endostyle (*ed.*) extends anteriorly to beyond the second intermuscular zone and posteriorly to the middle of the fourth zone. The anterior margin of the peripharyngeal band (*p.b.*) approaches the posterior margin of muscle I. The ciliated groove (*c.g.*) is situated in the center of the second intermuscular zone. The dorsal ganglion (*d.g.*) is located in the third intermuscular zone near the posterior margin of muscle III. The gill septum (*g.*) attaches at muscle IV dorsally at the middle, or slightly beyond, the fourth intermuscular zone ventrally. It bears about 50 pairs of elongate stigmata.

The loop of the alimentary canal is situated vertically in the fifth intermuscular zone with the oesophageal opening (*oe. op.*) on the sagittal plane. The stomach is elongate and rectangular in outline with the anterior margin slightly convex. The hind-stomach is very distinct with an extreme constriction between it and the intestine. The anus is located near the cardiac end of the stomach.

The ovary (*ov.*) is situated just in front of muscle VII. The testis (*t.*) projects anteriorly along the left side of the endostyle with its anterior portion often curving dorsally along the posterior side of the peripharyngeal band.

Doliolina undulata Tokioka and Berner 1958
Fig. 4

Doliolina undulata Tokioka and Berner, Pacific Sci. 12(2):135–138.

Several more specimens of *D. undulata* have been found in the material from the Shellback Expedition. In some of these, most frequently small mature specimens, the testis is stretched obliquely between muscles V and VI with

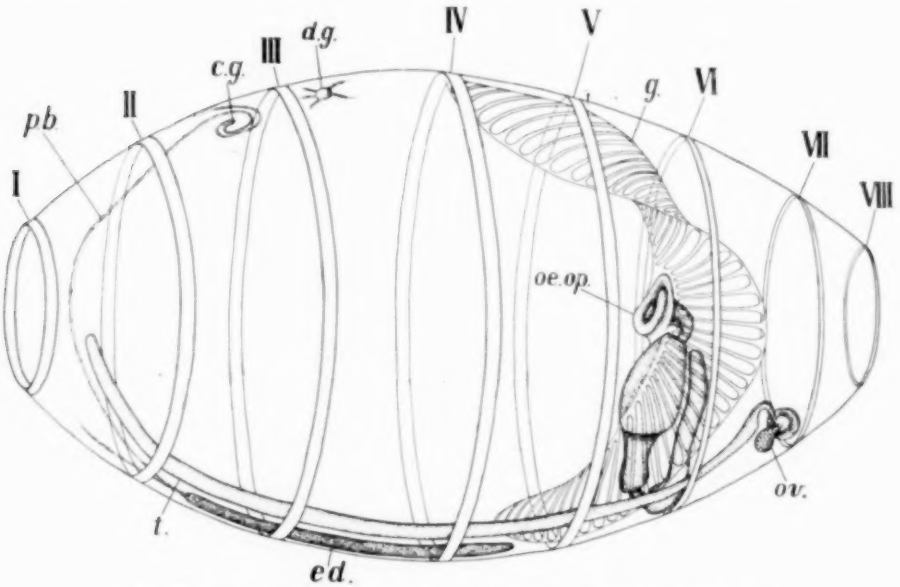

FIG. 3. *Doliolina intermedia* (Neumann) 1906, a 10 mm. gonozooid from left side.

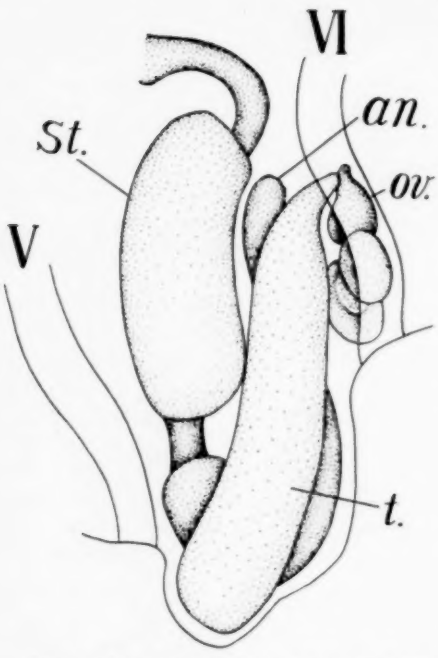

FIG. 4. *Doliolina undulata* Tokioka and Berner 1958, alimentary organs and gonads, from left side.

very little undulation. In these cases the ventral part of the body, just posterior to muscle V, is distended by the testis. The appearance of the testis and its relative position against the intestinal loop are fundamentally the same as in specimens with the undulating testis.

Subdivisions of the genus DOLIOLINA

With the descriptions of *D. undulata* Tokioka and Berner (1958) and here of *D. obscura* and *D. separata*, we find two types of muscle pattern within the genus *Doliolina*. These patterns, one in which all of the muscles form complete loops and one in which the seventh muscle is interrupted ventrally, distinctly divide the genus into two groups. On this basis we have established the following subdivision of the genus:

1) *Doliolina* perfecta: The muscle bands of this group all form complete bands. The following species are included: *indica* (Neumann 1906), *intermedia* (Neumann 1906), *resistible* (Neumann 1913), *mülleri* (Krohn 1852), *krohni* (Herdmann 1888), and *sigmoides* Garstang 1933.

2) *Doliolina* imperfecta: Within this group the seventh muscle band is always interrupted at the mid-ventral line. The species in this group are known only from the eastern Pacific Ocean, and include: *undulata* Tokioka and Berner 1958, *separata* n. sp., and *obscura* n. sp.

The shape and position of the gonad and the arrangement of the gill septum vary considerably within the two groups, and in some cases convergence of these features may be seen. We thus hesitate to treat them as subgenera of *Doliolina* but feel the problem may better be settled by more extensive collections and further critical examination of the respective species.

The discovery of three species of doliolids, in addition to the one previously known (*Dolioletta mirabilis*), in which a body muscle is interrupted gives support to the argument for the abandonment of the ordinal name Cyclomyaria for the doliolids, in favor of the name Doliolida. This change has been generally accepted since Garstang's review (1933).

Doliopsoides horizoni Tokioka and Berner 1958

Figs. 5A, B

Many additional specimens of *D. horizoni* have been found in the material from the Shellback Expedition. In some of these the alimentary organs are better preserved than in any of the previous specimens. Close examination of these organs reveals that the stomach is provided with several fingerlike protuberances. In one especially well-preserved specimen, four pairs of these protuberances were found on the ventral, posterior portion of the cardiac stomach and two pairs on the ventral, posterior portion of the pyloric stomach. The number of protuberances is not constant among the specimens.

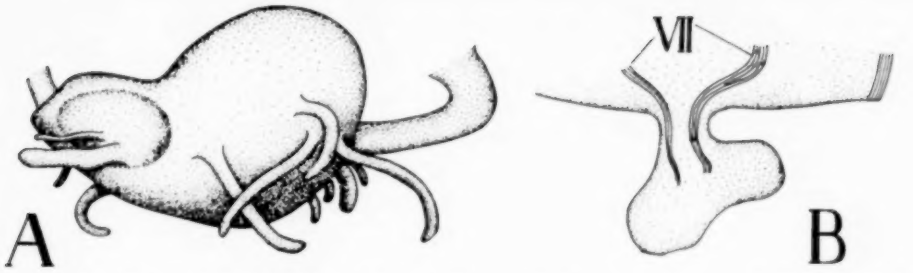

FIG. 5. A, *Doliopsoides horizoni* Tokioka and Berner 1958, stomach showing protuberances. B, *Doliopsoides horizoni*, ventral protuberance of phorozooid.

One individual of the phorozooid generation was found among the specimens. It has a short ventral protuberance into which both ends of muscle VII project.

COMPARISON OF ALIMENTARY REGION OF *Cyclosalpa strongylenteron* AND *C. bakeri*

In the examination of aggregate individuals of *Cyclosalpa strongylenteron* Berner 1955, some distinct asymmetries were found in the arrangement of the alimentary organs and gonads. These features differed somewhat between the dextral and sinistral individuals, although the musculature showed almost complete symmetry. The features of the alimentary organs and the gonads are compared with those of the aggregate form of *C. bakeri* Ritter 1905, whose visceral portion closely resembles that of *C. strongylenteron*.

In *Cyclosalpa strongylenteron* Berner 1955 (Figs. 6A, B, 7) the dextral individuals are those derived from the right side of the stolon when it is placed so that the stolo-individuals are situated dorsal side up, with the posterior end toward the right and with the proximal end of the stolon pointing away from the observer. The sinistral individuals are those derived from the left side of the stolon.

In the dextral individuals the intestinal loop is U-shaped. The anus (*an.*) opens on the left side at a level slightly anterior to the oesophageal opening (*oe. op.*). There is a large elongate blind sac or caecum (*l.c.*) attached to the ventral side of the lower branch of the loop, about one third of the way between the oesophageal opening and the posterior margin of the loop. The tip of the caecum reaches posteriorly nearly to the posterior margin of the gut loop but seldom beyond it. A small sac or protuberance (*r.c.*) is found on the left wall of the alimentary tract just dorsal to the base of the large caecum (Fig. 7). The duct of the circum-intestinal gland (*d.c.g.*) opens into the tip of this small sac, which could be considered merely a swelling of the proximal end of the duct. It is clear, however, that it is actually a projection of the alimentary tract. The swollen portion is stained reddish orange by Rose Bengal, like the alimentary tract, rather than purplish red like the duct. The relative positions of the small and large sacs indicate that they are the right and left caeca respectively.

The testis (*t.*) is about half the length of the left caecum and is situated on the right side of the ventral branch of the intestinal loop near its posterior margin. The vas deferens (*v.d.*) crosses the duct of the circum-intestinal gland on the left side and opens into the atrial cavity just in front of the point where the dorsal visceral muscles (*l.x.* and *r.x.*) from each side unite. These joined muscles project posteriorly into the center of the intestinal loop passing to the right of both the vas deferens and the duct of the circum-intestinal gland. The left visceral muscle (*l.x.'*) runs along the ventral side of the intestinal loop,

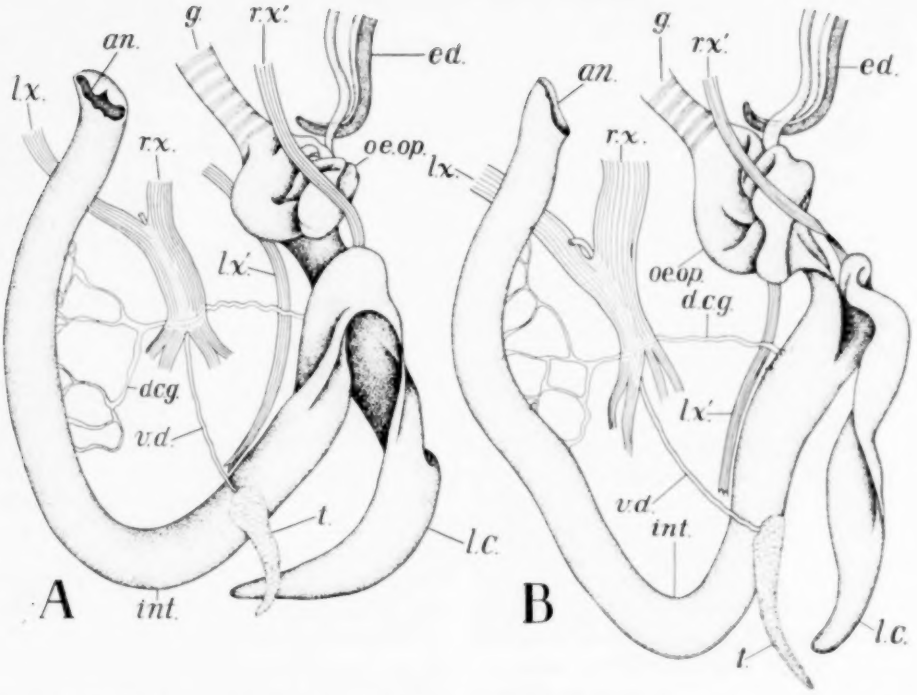

FIG. 6. A, *Cyclosalpa strongylenteron* Berner 1955, visceral region of the aggregate form, sinistral individual, from the right side. B, Same for dextral individual.

Abbreviations: *an.*, anus; *d.c.g.*, duct of the circum-intestinal gland; *ed.*, endostyle; *em.*, embryo; *g.*, gill; *ht.*, heart; *int.*, intestine; *l.c.*, left blind sac; *l.o.*, luminous organ; *l.x.*, left dorsal visceral muscle; *l.x'.*, left ventral visceral muscle; *oe.*, oesophagus; *r.c.*, right blind sac; *r.x.*, right dorsal visceral muscle; *r.x'.*, right ventral visceral muscle; *t.*, testis; *v.d.*, vas deferens.

crosses the duct of the circum-intestinal gland on the left side, and extends to near the base of the testis. The right visceral muscle (*r.x.'*) extends along the left side of the left caecum to a point near its posterobasal portion.

In the sinistral individuals the small right caecum is completely missing. The left caecum turns across the alimentary tract on the right side as shown in Figure 6A. The duct of the circum-intestinal gland opens at the base of the left caecum. Other structures are the same as in the dextral individuals.

The asymmetries found in the relation between the large (left) caecum and the small, or absent, right caecum, the arrangement of the testis, vas deferens, duct of the circum-intestinal gland and the visceral muscles, are all of a primary character. The twist of the left caecum, shown in the sinistral individuals, may be considered to have been brought about by enatiomorphism.

The structure of the intestinal loop of the aggregate form of *Cyclosalpa bakeri* Ritter 1905 (Fig. 8) closely resembles that of the aggregate form of *C. strongylenteron*. It is U-shaped, with the anus (*an.*) opening on the same level as the oesophageal opening (*oe. op.*). The right caecum is absent in both the dextral and the sinistral individuals. In the dextral individuals the left caecum (*l.c.*) is attached ven-

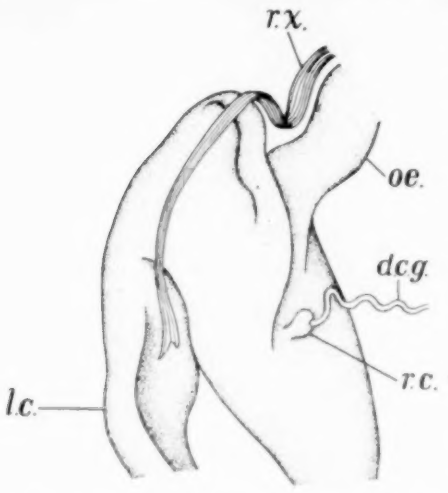

FIG. 7. *Cyclosalpa strongylenteron* Berner 1955, basal portion of left blind sac from left side.

trally about two thirds of the way down the lower branch of the intestinal loop. Its distal end reaches far beyond the posterior margin of the loop. In the sinistral individuals the caecum is twisted counterclockwise around the alimentary tract, as in the case of the sinistral individuals of *C. strongylenteron*. In the dextral individuals the duct of the circumintestinal gland (*d.c.g.*) opens into the intestine on the left side at the level of the anteriobasal portion of the caecum. In the sinistral individuals it opens into the base of the caecum itself.

The testis (*t.*) is held completely within a posterior protuberance projecting from the posterior portion of the intestinal loop. It is considerably longer than in *C. strongylenteron*. The vas deferens runs across the right side of the intestine, crosses the duct of the circumintestinal gland on the left side, and opens into the atrial cavity at a position far anterior to the anus.

The right visceral muscle (*r.x.*) runs down the right side of the intestinal loop to its posterior margin. The left visceral muscle (*l.x.*) projects deep into the posterior protuberance with the testis. In the dextral individuals the caecum is superficially placed in the median plane and asymmetry can be found only in the arrangement of the vas deferens and the difference in length of the visceral muscles. Such asymmetries are all of a primary nature.

If the structure of the visceral regions of the aggregate forms of *C. bakeri*, *C. strongylenteron*, and *C. virgula* are compared, we may be able to say to which *C. strongylenteron* is more closely related. On this basis it occupies an intermediate position between *C. virgula*, which has the small right caecum in both the dextral and sinistral individuals, and *C. bakeri*, in which the right caecum is lacking in both individuals. If, however, the musculature is phylogenetically more important than the structure of the visceral portion of the body, the above hypothesis is untenable.

During the examination of *C. bakeri* two

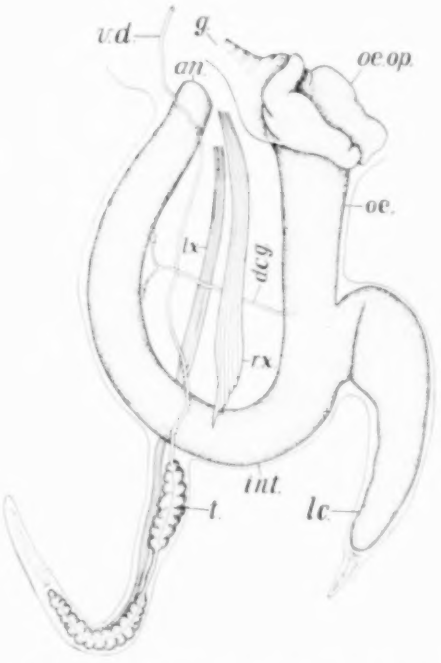

FIG. 8. *Cyclosalpa bakeri* Ritter 1905, visceral portion of dextral individual, from right side.

individuals of the aggregate generation were found which appeared to have light organs (Fig. 9). The organs were situated midlaterally, one on each side of the body between muscles II and III. This is the first report of possible light organs in the aggregate generation of *C. bakeri*.

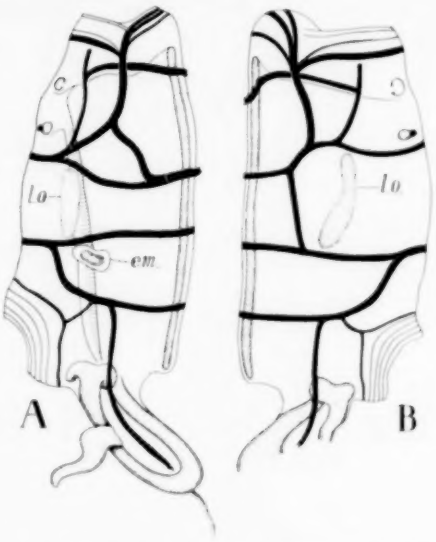

FIG. 9. *Cyclosalpa bakeri*, a 12 mm. aggregate form showing placement of luminous organ. A, from right side; B, from left side.

SUMMARY

Two new species in the genus *Doliolina*, *D. obscura* and *D. separata*, have been described. The genus *Doliolina* has been subdivided into two groups. The first is the *Doliolina* perfecta, in which all the muscle bands form complete loops, the second the *Doliolina* imperfecta, in which the seventh muscle band is interrupted ventrally.

The presence of fingerlike protuberances on the stomach of *Doliopsoides horizoni* have been described. Specimens of *Doliolina undulata* in which the undulations of the testis are much reduced are described. This straightening of the testis appears to be associated with early maturity.

Doliolina intermedium is reported from the central and tropical Pacific Ocean. The specimens differ from those previously described in having a slightly longer testis and in the nearness of the ovary to muscle VII.

The structure of the intestinal region of *C. strongylenteron* and *C. bakeri* are reviewed. On the basis of the structure of this region *C. strongylenteron* is placed in a position intermediate between *C. bakeri* and *C. virgula*.

The presence of what appear to be light organs in the aggregate generation of *C. bakeri* is noted.

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A Review of the Labrid Fish Genus *Labroides*, with Descriptions of Two New Species and Notes on Ecology[1]

JOHN E. RANDALL

AN INDO-PACIFIC genus of small labrid fishes (wrasses), *Labroides* Bleeker, is here restricted to four species, two of which are described as new from islands of the tropical central Pacific. Underwater observations of all of the species have revealed the unusual food habit of removal of ectoparasites from other fishes. This is discussed for each species in the accounts following taxonomic considerations.

Günther (1862: 120) and Fowler (1949: 117) considered *Diproctacanthus xanthurus* Bleeker in the genus *Labroides*. I am in agreement with de Beaufort (1940: 19, 151, fig. 26) that the monotypic *Diproctacanthus* Bleeker is a valid genus. *D. xanthurus* lacks the characteristic bilobed lower lip of *Labroides* and has two instead of three anal spines.

Smith (1957: 100, 104) established a new genus, *Fowlerella*, for *Labroides bicolor*, principally on the basis of fewer lateral line scales than *dimidiatus*. In view of the similarity of *bicolor* to *dimidiatus* in other respects than number of scales, I refer *Fowlerella* to the synonymy of *Labroides*.

Smith included *Labrus quadrilineatus* Rüppell (1835: 6, pl. 2, fig. 1) from the Red Sea with *dimidiatus* in the genus *Labroides* even though its scale counts would seem to ally it with *bicolor*. Actually *quadrilineatus* probably does not belong in *Labroides*, for this species has a completely scaled head (whereas in *Labroides* the head is naked except for suborbital, postorbital, and opercular regions), a slightly emarginate caudal fin, eight instead of nine dorsal spines, and in Rüppell's moderately detailed description there is no mention of a bilobed condition of the lower lip. Fowler (1928: 331) (after Schmeltz) also placed *quadrilineatus* in *Labroides* and listed it from Samoa. I am dubious of this record. Possibly Schmeltz obtained the young of *Labrichthys cyanotaenia* Bleeker which have two lengthwise pale bands on the body (although these are lower on the body of *cyanotaenia* than they are on *quadrilineatus* and the more ventral band is not as distinct). *Labrichthys unilineata* (Guichenot) from Guam is probably a synonym of *Labrichthys cyanotaenia*, based on this juvenile color pattern.

Saville-Kent (1893: 308, col. pl. 16, figs. 4, 9) described two species of *Labroides*, *L. bicincta* and *L. auropinna*, after seeing them in coral pools of Lady Elliot Island reef in the Great Barrier Reef of Australia. He obtained no specimens, but preferred to "provisionally" give the fishes new names. Although the color drawings on which these names are based are crude, it seems very likely that the blue and black *L. bicincta* is a juvenile *L. dimidiatus*. Saville-Kent mentioned its "resemblance to the white and black banded *L. dimidiatus*, C. and V." Obviously he was not aware that the true life color of *L. dimidiatus* is blue and black. The figure of *L. auropinna*, a blue fish with yellow fins, fits no known species of *Labroides*. Until a more complete description with necessary meristic, measurement, and detailed descriptive data on the species is available, I prefer not to recognize this name. It is possible that *L. auropinna* is not a species of *Labroides*, and perhaps not even a labrid.

[1] Contribution No. 209 from the Marine Laboratory, University of Miami, Miami, Florida. Manuscript received October 16, 1956.

The genus *Labroides* is distinguished from other genera of the Labridae in having a small mouth with thick lips, the upper with a shallow median groove and the lower divided into two prominent, anteriorly projecting lobes. The inner surface of the lips has fleshy folds. There is a single pair of large, curved, canine teeth anteriorly in each jaw, the upper pair fitting inside the widely-spaced lower pair when the mouth is closed. There is a large, anteriorly directed, canine tooth at the extreme posterior part of the upper jaw, separated by a gap from anterior teeth. The remaining teeth are small, those in the lower jaw in several close-set rows between the canines and those in the upper jaw forming a large mass just behind the anterior canines, this mass with a marked indentation anteriorly in the mid-line. The body is compressed, its width contained about 2.5 to 3 times in the head length, and moderately elongate, its depth contained about 3.5 to 4 times in the standard length. The caudal fin is truncate or slightly rounded. The preopercle is entire, its margin smooth. The gill membranes are attached to the isthmus. The snout is pointed. The snout, entire dorsal surface of the head, chin, and throat are scaleless. The lateral line is continuous, and the lateral line scales number 28 or 52 to 54. Fin ray counts are as follows: D IX, 11 or 12; A III, 10; P 13 (uppermost two rays unbranched). The species are small, individual fish usually being less than 100 mm. in standard length.

KEY TO THE SPECIES OF LABROIDES

(Applicable primarily to adults; see discussion below concerning juveniles)

1a. Lateral line scales 52 to 54; color light blue with a median lateral black band from snout to end of caudal fin (this band broadening as it passes posteriorly on body) (Indo-Pacific) . . . . . **Labroides dimidiatus**

1b. Lateral line scales 28; color not as above (although a median lateral black band is often distinct anteriorly on body and on head) 2

2a. Snout long, diameter of eye contained 2.1 to 2.5 times in snout length; caudal peduncle and caudal fin pale with a prominent black crescent posteriorly in fin, the attenuate ends of which extend to margins of caudal peduncle (tropical Pacific) . . . . . **Labroides bicolor**

2b. Snout not long, diameter of eye contained 1.5 to 1.9 times in snout length; caudal peduncle and caudal fin black with upper and lower edges of fin pale 3

3a. Median lateral black band which extends posteriorly from snout continuous with black posterior half of body; no dusky streak on cheek below eye; pale edges of caudal fin magenta in life; maximum standard length in excess of 80 mm. (Hawaiian Islands) . . . . . **Labroides phthirophagus,** n. sp.

3b. Median lateral black band which extends posteriorly from snout merges gradually to broad, pale-brown (dull-orange in life) area in center of body; a narrow dusky streak on cheek below eye running from chin to base of pectoral (may be faint in small adults); pale edges of caudal fin light lavender in life; maximum standard length about 60 mm. (Society Islands and Tuamotu Archipelago) . . . . . **Labroides rubrolabiatus,** n. sp.

Juvenile specimens for all species are unavailable to me; however, all have been viewed underwater, frequently in the proximity of adults. Juveniles of all four species appear to have the same basic color pattern, namely black with a broad band of color along the back which extends and narrows on to snout. On *L. dimidiatus* and *L. rubrolabiatus* this band is brilliant deep blue (these species are readily separable by scale counts; see key above); on *L. bicolor* it is bright yellow; on *L. phthirophagus* it is bright purple.

Labroides dimidiatus
(Cuvier and Valenciennes)
Fig. 1

Labrus latovittatus Rüppell, (*non* Lacépède), 1835, Neue Wirbelth., Fische . . . , p. 2.
Cossyphus dimidiatus Cuvier and Valenciennes, 1839, Hist. Nat. des Poiss., vol. 13, p. 136.
Labroides paradiseus Bleeker, 1851, Natuurk. Tijdschr. v. Nederland. Indië, vol. 2, p. 249.
Labroides bicincta Saville-Kent, 1893, The Great Barrier Reef of Australia, p. 308, pl. 16, fig. 4.
Labroides caeruleo-lineatus Fowler, 1945, Acad. Nat. Sci. Phila., Proc., vol. 97, p. 65, fig. 7.

TYPE LOCALITY: Mauritius.

This blue and black species is the most common and widespread of the genus, ranging from Africa to the tropical Pacific (where it is recorded from most major island groups).

Labroides paradiseus Bleeker differs from *dimidiatus* in having a hooklike ventroanterior extension of the broad black band in the caudal fin. I have observed various degrees of intermediacy between typical *dimidiatus* and the *paradiseus* form, and I regard the latter as a color variety, as did Günther (1881: 243). In the Society Islands and Tuamotu Archipelago I have seen no specimens of the *paradiseus* variety, although collections are not extensive. In large collections from the Marshall Islands and the Philippines in the United States National Museum the *paradiseus* form predominates.

At Makatea and Takaroa in the Tuamotu Archipelago, and to a lesser extent at Tahiti and Moorea, another color variant was observed. Occasional adults have a dull red-orange region in the middle of the body below and adjacent to the median black band. In the Marquesas *L. dimidiatus* were seen with a red-orange area which was longer and occurred above as well as below the black band.

Barnard (1927: 749) described two color varieties of the species at Natal, East Africa, one with a dark stripe across the base of the pectoral fin and one without. He stated that the color of the species in Africa is blue or yellow with a black longitudinal band. Smith (1949: 291), also reporting on the species from East Africa, described the color as varying rapidly from light pink through straw yellow to dark blue, apparently at will and according to the emotional state of the fish. I have never seen *L. dimidiatus* in the Pacific pink or yellow instead of blue, nor have I observed any rapid color changes. With age there is a loss of brilliance and a lightening of the blue color. Below the median black band large adults are nearly white.

A juvenile specimen, 24 mm. in standard length, collected by the author in Tahiti, was colored in life as follows: black with a band of deep blue about a pupil diameter in width beginning at upper lip and passing backward through upper part of eye (lower edge of band at upper edge of pupil) on to nape, where it is nearly two pupil diameters in width, and thence on to back, where it gradually narrows until it terminates dorsally on caudal peduncle; the black middorsal region, which is bordered by a blue band on each side, is broadest on the head and narrows as

FIG. 1. *Labroides dimidiatus*, 83 mm., Society Islands. Caudal fin not expanded, hence emarginate appearance.

it passes posteriorly until it ends at rear of dorsal fin; head and thorax below level of lower edge of eye are pale; caudal fin black with narrow pale-violet edges; dorsal and anal fins dusky basally and hyaline distally, the dorsal blackish anteriorly, the anal darker posteriorly; paired fins pale.

Labroides caeruleo-lineatus Fowler (1945: 65, fig. 7) (1946: 159) is a young *L. dimidiatus*. The description was based on a 28 mm. specimen, and the figure clearly shows the typical juvenile color pattern as described above.

L. dimidiatus occurs most commonly in coral or coral-sand areas which are protected from wave action. Around atolls individuals are most often seen in lagoons rather than outside the peripheral reefs. I have observed them in water as shallow as 2 feet and as deep as 120 feet, but they appear to be more abundant in shallow water. Regan (1908: 230) has recorded the species from 34 fathoms in the Maldives.

Of this species de Beaufort (1940: 148) wrote, "In the aquarium of Amsterdam I observed that *Labroides dimidiatus* cleans the surrounding of the mouth and the gill openings of large fishes (Het Aquarium IV, 1936: 153) in the same way as has been observed by Beebe for the Atlantic species *Iridio bivittatus*." Smith (1949: 291) stated that *L. dimidiatus* "Feeds on minute organisms on rocks and has been observed to nibble over the mouth parts and gill covers of large Rock-cods." Doty and Morrison (1954: 24) observed what they termed an interesting association between a parrot fish and a fish which is undoubtedly *L. dimidiatus*.[2] The latter "cleans off its larger companion's beaklike jaws, teeth and head area." They implied that this unusual association is limited to just these two species; however, I have observed (Figs. 2, 3, 5) *L. dimidiatus* picking at the heads, bodies, and fins of numerous species of reef fishes representing many different families, including the carangids and serranids, members of which habitually prey upon small reef fishes.

None of the above authors mentioned the removal of ectoparasites; the use of the term cleansing gives the connotation of removal of debris or particles of food.

The stomach contents of two specimens from the Gilbert Islands and three from the Marshall Islands consisted of calagoid copepods which are ectoparasitic on fishes; two more specimens from the Gilberts had eaten small isopods (also fish parasites) along with a few fish scales (Randall, 1955*b*: 144). Subsequently, a specimen, 72 mm. in standard length, from Hull Atoll, Phoenix Islands, was found to contain three caligid copepods

FIG. 2. A parrot fish, *Scarus* sp. (upper fish), and a surgeon fish, *Zebrasoma scopas* (lower fish), each being examined for ectoparasites by *Labroides dimidiatus*. Reproduced from 16 mm. movie film taken in the lagoon of Takaroa, Tuamotus.

[2] These authors erroneously refer to this species as a blenny—probably because of the confusion that results from the similarity in color pattern of *L. dimidiatus* to the blenny *Aspidontus taeniatus* Quoy and Gaimard, a similarity so striking that Barnard (1927: 749) suggested that mimicry might be involved, with perhaps one or the other species being poisonous. R. W. Hiatt and D. W. Strasburg observed the resemblance at Arno Atoll in the Marshall Islands and suspected mimicry. Randall (1955*b*: 144), noting it in the Gilbert Islands, proposed that the blenny might be mimicking the labrid, since the latter might gain protection from predaceous fishes by virtue of its food habits.

FIG. 3. A pair of *Labroides dimidiatus* picking at the wrasse *Epibulis insidiator*. Reproduced from 16 mm. movie film taken in the lagoon of Takaroa, Tuamotus.

and three small fish scales in the stomach and the digested remains of numerous calagoid copepods in the intestine. A 71 mm. specimen from the Society Islands had two calagoids in the stomach and four calagoids and one larval gnathiid isopod in the intestine. One section of the intestine had a bit of soft bottom debris including a few fragments of algae. A 65 mm. specimen from the Society Islands had an empty stomach and the remains of 13 calagoid copepods and 1 lernaeid copepod in the intestine. A 24 mm. juvenile had eaten five small larval gnathiid isopods and three immature calagoid copepods. Nonparasitic crustaceans were not found in any of the specimens examined. The bottom debris in the one specimen may indicate occasional feeding on free-living forms, however, the species appears to be at least dominantly a feeder on crustacean ectoparasites of fishes.

Although Doty and Morrison (*op. cit.*) stated that parrot fish were feeding when the labrid cleansed them, host fishes are generally not so oblivious to having their parasites removed. Usually the fishes display some distinctive behavior during the process. Often they remain completely motionless in the water, although they may swim slowly. Usually their fins are fully erected (this may be associated with the high percentage of crustacean parasites which occur on the fins as compared with the rest of the body epidermis), and there may be a disorientation of the body to a position out of the vertical plane (i.e., tilted to one side) or with the anterior part of the body elevated. At times color changes are apparent. The black-hued surgeon fish *Acanthurus achilles* Shaw, for example, may become bright blue when picked over by *Labroides*.

Of all of the species of *Labroides*, *L. dimidiatus* is the least wary and will often swim up to a human observer, sculling along by pectoral fins alone in typical wrasse fashion, as if to investigate the possibility of human ectoparasites. I have experienced a picking at the hairs of my legs by this species and on one occasion a persistent and vigorous nipping at a small mole on my chest.

Randall (*op. cit.*) noted a peculair mode of swimming often displayed by *L. dimidiatus* when near other fishes, describing it as an oscillation of the posterior part of the body during slow progression. Doty and Morrison wrote that this species swam "in an odd leaping fashion, somewhat like a finch in flight." I presume that this "dancing" about other fishes by this and other species of *Labroides*, coupled with their remarkable color, serves to enhance their recognition by the other fishes. Further, I noted in the Society Islands that *L. dimidiatus*, when near other fishes, often elevates its dorsal fin, especially anteriorly, such that the black forward part of the fin appears like a conspicuous black triangle.

On several occasions I have seen *Labroides dimidiatus* enter the buccal and gill cavities of larger fishes, ostensibly to remove parasites. Probably this occurs more often than these few observations suggest, for the proximity of a swimmer appears to frighten the host fishes sufficiently to preclude their entering

into this more complex symbiotic association. In Papetoai Bay, Moorea, at a depth of 20 feet, about a 200 mm. *Parupeneus trifasciatus* (Lacépède) approached an adult *L. dimidiatus*. As it neared the latter, it changed its color rapidly from light tan to mottled pink. The *Labroides* picked over the body and fins of this goatfish, moving anteriorly. When it reached the forward part of the head, the goatfish opened its mouth and the wrasse inserted more than half of its body into the mouth and remained there several seconds. Subsequently two adult goatfish of the species *Mulloidichthys samoensis* (Günther) interrupted the pair and received the attention of the *Labroides*. D. W. Strasburg has written that he made the same observation with *L. dimidiatus* and *P. trifasciatus* at Eniwetok Atoll in the Marshall Islands. In Teavenui Pass, Bora Bora, Society Islands, at a depth of about seven feet, I saw a 1240 mm. moray eel (*Gymnothorax javanicus* Bleeker) with its head and anterior third of its body projecting from beneath a coral ledge. It was being picked over by a *L. dimidiatus* about 50 mm. long. After about 30 seconds the wrasse devoted its attention to the eel's head, whereupon the latter opened its mouth widely, maintaining it in this position for about eight seconds while the labrid picked inside the upper and lower jaws and then disappeared back into the pharynx. A sharp lateral jerk of the eel's head preceded the departure of the wrasse. The eel was then speared to permit positive identification. A similar observation was made at Takaroa in the Tuamotus. The eel appeared to be the same species and the *L. dimidiatus* was a juvenile about 20 mm. in length. At Caroline Atoll (10° S., 150°14′ W.) I saw an adult *L. dimidiatus* slip the anterior third of its body into the gill cavity of the chaetodontid *Hemitaurichthys thompsoni* Fowler by way of the gill opening. The latter held its opercula open without respiring for several seconds to accommodate the labrid. In the Tuamotus individual *L. dimidiatus* were observed to enter the gill cavities of the wrasse *Epibulis insidiator* (Pallas), the grouper *Variola louti* (Forskål), and the goatfish *Parupeneus barberinus* (Lacépède) via the gill openings.

Labroides dimidiatus are frequently seen in pairs. Also it has been noted that individual fish or pairs of fish appear to remain around the same small coral head or small section of a larger reef. The fish described above in association with *Parupeneus trifasciatus* is one of a pair which has been sighted in the same area over a period of six months. Other pairs or individual fish have been observed to be restricted to small areas.

If a parasite-feeding fish is resident to a small section of bottom and other fishes in the area are nonmigratory (probably true for the majority of coral reef fishes), its food supply would be insufficient, for it would be limited to the ectoparasites of fishes in its immediate surroundings. Therefore, it was not surprising to note that fishes come from beyond the range of vision to a *Labroides* site. A school of subadult *Mulloidichthys samoensis* was consistently seen to occupy a region of sandy bottom over 50 feet from the shore reef where the pair of *L. dimidiatus* mentioned above could be found. As I watched, small groups of about eight of the goatfish moved toward the *Labroides* site and remained in the area until they had been picked over; then they would return to their usual place. Their swimming back and forth from where the school congregated to where the *Labroides* were resident was not haphazard but directional, even though the water was not clear enough for me to see the reef from where the school was situated. Another species which swam to these two labrids from a locality previously known to me was a large adult *Abudefduf septemfasciatus* (Cuvier and Valenciennes), the only one of its size in the area. The rocks along the shore where it habitually hid are 45 feet from the labrid locale. *Caranx melampygus* Cuvier and Valenciennes, a foot or more in length, were other visitors which came to be "serviced" and left when the service had been finished. These fish are what

might be termed roving carnivores and appear to move over considerable distances. Yet they seemed to know the *Labroides* site, for they would come up to it from deeper water of the bay. At the atoll of Takaroa in the Tuamotus a four-foot moray eel (*Gymnothorax javanicus*) was seen to leave a hole in the coral, swim 15 feet over the bottom to a small coral head where a *Labroides dimidiatus* was located. There it was picked over the head and body by the labrid, after which it returned to the hole. Other fishes, such as *Ctenochaetus striatus* (Quoy and Gaimard), which were commonly seen being nibbled at by *L. dimidiatus*, could not be distinguished from one another or identified as having come from a certain area; nevertheless, it is expected that some means of marking many such fishes in the area, such as with different colored tags, would demonstrate that these fish are aware of the place where the *Labroides* can be found and swim there, perhaps under the stimulation of being irritated by ectoparasites. Individual *L. dimidiatus* are not wholly dependent on fishes bearing parasites coming directly to them. Often the species has been observed swimming over the reef for distances as great as 60 feet "servicing" fishes on the way. This was especially true in areas where the highly territorial damsel fish *Pomacentrus nigricans* (Lacépède) was common. As one damsel fish was being tended, another nearby would assume a stationary pose with fins erect and the *Labroides* would move on to the latter with little hesitation. For further discussion of the subject of restricted "home" sites of *Labroides*, as applicable to *L. phthirophagus*, see the account of this species.

The habit of feeding on ectoparasites is not unique to the genus *Labroides*, as might be surmised from the reference above to the labrid *Iridio* (=*Halichoeres*) *bivittatus* of the Atlantic. Longley (in Longley and Hildebrand, 1941: 129) reported that small porkfish, *Anisotremus virginicus* (Linnaeus), nibble and peck at the surfaces of larger fishes at Tortugas. I was fortunate to observe one individual of this species pecking at the body of the Nassau grouper, *Epinephelus striatus* (Bloch), in Florida, and can thus corroborate Longley's observation. In addition, I saw a juvenile of the pomacentrid *Microspathodon chrysyrus* (Cuvier and Valenciennes) picking over the fins and body of an angel fish, *Pomacanthus arcuatus* (Linnaeus), which remained nearly motionless during the process. Also suspected of feeding on ectoparasites of fishes by Longley are the goby *Elacatinus oceanops* Jordan (p. 226) and the young of the labrid *Thalassoma bifasciatum* (Bloch) (p. 198). Of the former he wrote, "Wherever found, these small fish slip out from shelter, attach themselves by their ventral disks to other fishes, and 'creep' over them, presumably to look for parasites. As many as 6 have been seen together on a *Mycteroperca venenosa* about ½ yard long. . . . The boldness of these tiny fish is almost incredible. They will creep over the teeth of the great *Pseudoscarus*, or enter the mouths of grunts and groupers and explore them with unhurried movements. . . . Their attentions usually continue until the larger fishes grow restless, start up abruptly, or move away and leave them, whereupon they return to their original stations."

Interestingly, the color of this goby is similar to that of *Labroides dimidiatus*. *E. oceanops* which I observed in Florida were blue with a black longitudinal band running from the snout through the lower part of the eye, broadening on the body, and ending on ventral half of caudal fin.

A recent paper by Eibl-Eibesfeldt (1955) is devoted in a large part to the detailed observation of the behavior of fishes which "cleanse" larger fishes. He observed the following species in the Caribbean in symbiotic association with larger fishes: *Elacatinus oceanops*, young *Thalassoma bifasciatum*, young *Anisotremus virginicus*, young *Bodianus rufus* (Linnaeus) (Labridae), and *Gramma hemichrysos* Mowbray (Pseudochromidae). He noted that the larger fishes do not merely accept the cleansing but invite it by taking special posi-

tions. Furthermore he observed that the larger fish seek out the stations of the "cleaners." He made the following observation of *Elacatinus oceanops* and *Epinephelus striatus*. As soon as the grouper came close to the coral where the gobies were located, the little fish swam immediately in his direction and started to clean his body. Sometimes the grouper lay on his side. He allowed the gobies to enter and leave the buccal cavity through his mouth and gill openings which he held rigidly open. After about 30 seconds he respired once or twice and then opened his mouth and elevated his gill covers again. When he wanted to leave, he made a signal by closing his mouth sharply, although not completely, and then opening it widely. At this signal the gobies came out. Before leaving the grouper shook his body. Even if frightened (as by a diver) he still took time to make the signal to the gobies. Of the small fishes listed above which cleanse larger fishes, only *Elacatinus oceanops* and young *Bodianus rufus* were seen to enter the buccal cavity of larger fishes. Large fish were never observed trying to catch any of the little fish. Eibl-Eibesfeldt suggests that it be ascertained whether the appetite of predaceous fishes is first appeased before they allow themselves to be picked over by the smaller fishes. No mention was made of the examination of stomach contents for ectoparasites by this author.

Eibl-Eibesfeldt has informed me in a letter that he has since observed "*Coris giofredi* Risso cleaning a *Crenilabris*" in the Mediterranean south of Naples.

Szidal and Nani (1951: 412) examined the stomach contents of a *Remora remora* (Linnaeus) from the coast of Argentina and found four parasitic copepods of the family Caligidae, three of them males of *Achteinus dentatus* Wilson and the other a female *Pandarus;* both forms are known to parasitize sharks.

Hubbs and Hubbs (1954: 194) stated that the embiotocid *Brachyistius frenatus* Gill and the labrid *Oxyjulis californica* (Günther) have at times been observed feeding on ectoparasites of other California fishes.

The food habit of removal of ectoparasites from other fishes represents a distinct biological niche. It is interesting to note how different species, often from totally different families, have filled this niche in different areas of the world; however, more of them are species of Labridae than of any other family. It should be added that primarily tropical and subtropical areas, where labrids are usually numerous, have been investigated.

In addition to fishes like *Labroides*, certain shrimps have been observed removing ectoparasites from fishes. In Papetoai Bay and the lagoon of Moorea at depths of about 70 feet the author watched a shrimp picking at fishes. The shrimp was identified as *Hippolysmata grabhami* by Dr. F. A. Chace, Jr. The adult shrimp are about 40 to 50 mm. in total body length, have a brilliant red band along the back which is bisected by a white middorsal line, and long white antennae and antennules. They were seen on the surface of isolated blocks of coral. When fish approached they waved their antennae and antennules as if to attract the fish. Among the fishes seen to enter into symbiotic association with this shrimp were: *Apogon exostigma* (Jordan and Starks), *Apogon* sp., *Anthias* sp., juvenile *Acanthurus mata* (Cuvier), and *Gymnothorax flavimarginata* (Rüppell). A shrimp climbed on to a two-foot specimen of the latter species and busily picked over the dorsal part of the eel's head.

Labroides bicolor Fowler and Bean
Fig. 4

Labroides bicolor Fowler and Bean, 1928, U. S. Natl. Mus., Bul. 100, vol. 8: 224, pl. 18.

TYPE LOCALITY: Port Maricaban, Philippine Islands.

Judging from the few locality records of the species (Philippines, Java (Hardenberg, 1936), Japan (Kamohara, 1952), the Gilbert Islands (Randall, 1955*b*), Aldabra, Indian Ocean (Smith, 1955)), *L. bicolor* would ap-

FIG. 4. *Labroides bicolor*, 81 mm., Gilbert Islands.

pear to be rare, although wide-ranging in the Indo-Pacific. I can attest to its rarity at Onotoa Atoll in the Gilbert Islands, where two months of field work resulted in the sighting of only two individuals. Subsequently in the Society Islands and Tuamotu Archipelago I have found the species surprisingly common for the genus. The two fish at Onotoa were observed in clear water beyond the windward reef of the atoll. Dr. Leonard P. Schultz of the United States National Museum has informed me that he will record the species from the northern Marshall Islands in volume II of *Fishes of the Marshall and Marianas Islands*. His specimens were taken on reefs exposed to severe wave action. In the Society Islands and Tuamotus, however, the species has rarely been observed outside of the barrier reefs but occurs more often around reefs in protected lagoon and bay areas. The apparent difference in habitat between this fish in the Gilbert and Marshall islands and the Society Islands may be a manifestation of possible subspecific differentiation. Further collections and observations are needed to elucidate the problem. Specimens from the Society Islands and Tuamotus have been sent to the United States National Museum and the Natural History Museum, Stanford University. *L. bicolor* was observed but not taken from the Marquesas Islands.

Although only adults were collected, the abundance of *L. bicolor* at the island of Moorea enabled me to perceive marked color changes which take place from the juvenile to the adult stage. In the following account, the color of juveniles is based on underwater observation. Juveniles as small as about 15 mm. in standard length have been observed. From this size to about 30 mm. the fish appear entirely black except for a brilliant yellow band along the back above the midlateral line of the body (this band confluent with one on other side dorsally on caudal peduncle and caudal fin) which extends on to head, including upper edge of eye and narrows as it terminates on snout. At a length of about 30 mm. the same general color obtains but the caudal fin and posterior part of caudal peduncle become pale yellow or almost white; subsequently, at the posterior part of the caudal fin, a trace of the black crescent so typical of adults appears. Then the yellow band along the back is replaced by light gray (the brilliant yellow color persisting longest on the head), and a light-gray area appears ventrally, thus restricting the black body color to a broad band along the middle of the body and head. Concomitant with the appearance of gray color is the development of the black crescent in the caudal fin. Anterior to the crescent a greenish tinge appears, replacing the pale-yellow color. Curiously, the next trend is a darkening of the light gray above and below the black band on the head and body and an intensification and enlargement of the yellow area posteriorly on the body. At about 60 mm. the yellow area is defined but scales anterior to the caudal peduncle have blackish centers. It is not until a standard length of nearly

75 mm. is reached that this large elliptical region is bright yellow, free or nearly so of scales with dusky centers. The green on the caudal fin also intensifies and blue appears posterior to the crescent and on the outer part of the dorsal and anal fins. On large fish (the species is the largest of the genus, attaining a standard length slightly in excess of 100 mm.) a suffusion of dark blue becomes apparent anteriorly.

A 98 mm. specimen speared in Moorea provided the following color description: body black except for a broad yellow area posteriorly, the forward end of which is rounded and reaches a vertical through base of fourth soft ray of dorsal fin; head dark blue and lacking the prominent black lateral band; lips dark blue, shading to light blue on inner surfaces; caudal fin with a subterminal black crescent, bright green anterior to and blue posterior to this marking; dorsal and anal fins black with broad light blue edges; pectorals hyaline; pelvics black.

This specimen and another 94 mm. one with the same color are males. On other individuals as large as blue-headed ones seen underwater the dark midlateral band is visible on the head and the deep-blue color is lacking, although the head and anterior part of the body above and below the band are dark grayish blue. The largest of the latter color variety collected in the Society Islands is 80 mm. in standard length, and it is a female. It is believed that others may consistently prove to be females too. At times one of each color variety are seen together as a pair. The above-mentioned color differences, if conclusively demonstrated to be sexual, are slight compared to the degree of sexual dichromatism known in some of the Labridae (Randall, 1955*a*).

On numerous occasions in the Society Islands and Tuamotus individuals of this species, both juvenile and adult, have been observed picking at the bodies, heads, and fins of other fishes. The contents of the gut of eight specimens, 60 to 98 mm. in standard length, have been examined. Four were empty save for a mucuslike substance and, in the case of two of the specimens, tiny digenetic flukes in the intestine, which were probably internal parasites of these fish. A 69 mm. specimen had two calagoid copepods and one fish scale in the stomach; 65 and 80 mm. specimens were empty except for a few fish scales in the stomach and intestine. The stomach of a 60 mm. specimen was empty, but three small larval isopods of the family Gnathiidae (larvae of this family consist exclusively of fish parasites) were found in the intestine.

The presence of fish scales in the gut is comprehensible when the stout, curved, canine teeth and the vigor with which the little labrids nip the host fishes are considered. A medium-sized *L. bicolor* was seen to actually lift a piece of skin of an adult puffer, *Arothron meleagris* Bloch and Schneider, into a pronounced peak in its apparent effort to dislodge an ectoparasite.

The host fishes do not always tolerate such ardent pecking. Often they move their bodies sharply or swim away when the pecking becomes vigorous.

Adult *L. bicolor* do not display the oscillatory swimming movement as previously described for *L. dimidiatus*. The brilliant yellow and black young do, however. A further distinction between the behavior of young and adults lies in the tendency of the former to remain in a very restricted region, frequently a small cave or under a ledge. Adults are almost constantly on the move and appear to cover a larger area than other species of *Labroides*. Still, they seem to remain in the same general region. In addition to seeing what appeared to be the same individuals day after day at a certain reef, several which were wounded with a spear and could be positively identified were repeatedly sighted at approximately the same place.

As might be surmised from the above, adults of this species are more prone to seek out fishes from which to remove parasites

than the other species of the genus. They have been observed to follow individual fishes closely for 30 feet or more, frequently making contact with the dorsal fin or the dorsal part of the body of these fishes.

I have never observed *L. bicolor* enter the mouth or gill cavities of larger fishes as has been observed for *L. dimidiatus*, *L. phthirophagus*, and *L. rubrolabiatus*. *L. bicolor* is noticeably shyer than the other species, however, and individual fish usually swim away as a swimmer approaches; thus it is possible that such behavior occurs.

The three species of *Labroides* which are found in the Society Islands, Tuamotus, and Marquesas, *L. dimidiatus*, *L. bicolor*, and *L. rubrolabiatus*, are frequently seen near one another and rarely exhibit territoriality. On one occasion I observed all three together around a single small coral head. At Takaroa in the Tuamotus *L. dimidiatus* and *L. rubrolabiatus* were both seen to pick at the body of the parrot fish, *Scarus harid* Forskål, at the same time. In Moorea a five-foot moray eel of the species *Gymnothorax javanicus* was observed lying nearly motionless entirely in the open beside a small head of coral and being picked over simultaneously by two adult *Labroides*, one *L. dimidiatus* and the other *L. bicolor*. Until the small labrids were seen, the eel's position was perplexing, for morays are rarely seen free from their holes in the coral during the day unless in rapid transit from one hole to another. *L. dimidiatus* has thrice been observed to peck briefly at the bodies of adult *L. bicolor;* twice the *dimidiatus* were of about equal size as the *bicolor* (Fig. 5), and the remaining time definitely smaller.

Generally, individuals of the species of *Labroides* tend fishes larger than themselves, juveniles "taking care" of the smaller reef fishes. It is by no means rare, however, to see species of *Labroides* picking at fishes smaller than themselves. Conversely, tiny juveniles have been frequently seen busily working over the surface of fishes ten times or more their size. Several times *L. dimidiatus* 20 mm. or less in standard length have been seen in association with adult groupers (*Cephalopholis argus* Bloch and Schneider) 200 to 300 mm. in standard length and *L. bicolor* of about the same small size with full-grown squirrel fishes (*Myripristis* spp.).

FIG. 5. *Labroides bicolor*, (on right) being "serviced" by *L. dimidiatus*. Reproduced from 16 mm. movie film taken in the lagoon of Takaroa, Tuamotus.

At Takaroa an adult *L. bicolor* was observed to swim after a six-foot shark of the species *Triaenodon obesus* (Rüppell) and to make a few hasty pecks at the dorsal part of the body.

Labroides phthirophagus, new species
Pl. 1A

HOLOTYPE: U. S. Natl. Mus. No. 164466, a male specimen, 68.0 mm. in standard length and 84.0 mm. in total length, collected by J. Randall with a spear in 7 feet of water, about 100 yards offshore from the Waikiki branch of the Hawaii Marine Laboratory, Honolulu, Territory of Hawaii, on March 1, 1955.

PARATYPES: U. S. Natl. Mus. No. 164469, 69.0 mm. in standard length, collected by J. Randall with a spear in 5 feet of water in

Kealakekua Bay, Hawaii, on June 15, 1954; U. S. Natl. Mus. No. 164467, 83.5 mm. in standard length, collected with rotenone by W. Gosline and class at Diamond Head, Oahu, on Dec. 22, 1951; U. S. Natl. Mus. No. 164468, 18.8 mm. in standard length, collected with rotenone by W. Gosline and class at Diamond Head, Oahu, on Dec. 23, 1953; Stanford Univ. Mus. No. SU48445, 2 specimens, 64.5 and 69.0 mm. in standard length, collected by J. Randall with a spear in 18 feet of water at Waianae, Oahu, on Oct. 14, 1955; British Mus. No. 1955.12.12.1, 60.0 mm. in standard length, collected by J. Randall with a spear in 35 feet of water at Manana Island (Rabbit Island), Oahu, on Sept. 29, 1955.

In addition to the above, there is a series of 12 specimens, 19 to 76 mm. in standard length, in the collection of the University of Hawaii.

DESCRIPTION: Based on the holotype and the smallest (18.8 mm. in standard length, 23.2 mm. in total length) and the largest (83.5 mm. in standard length, 103 mm. in total length) paratypes. Counts and measurements are recorded for the holotype, followed in parentheses by data for the small and large paratypes, respectively. When counts of the two paratypes are the same as the holotype, only a single number is given.

Dorsal fin rays IX, 11; anal fin rays III, 10; pectoral fin rays 13 (the uppermost rudimentary, the next unbranched); pelvic fin rays I, 5; principal caudal rays 14. Lateral line scales 28, the last slightly enlarged and with a prominent lateral line tube; lateral line partially interrupted in adults (the lateral line in the 20th and 21st scales, the two which contain that part of the line which angles sharply downward at the level of the posterior part of the dorsal fin, is poorly developed; no degeneration in the lateral line at this location is apparent in the 18.8 mm. juvenile specimen, however). Scale rows above lateral line to base of first soft dorsal rays 3; scale rows below lateral line to base of first anal soft rays 8; median predorsal scales 8 (9 or 10 in large paratype and none in the juvenile specimen). Snout, chin, throat, and dorsal part of head naked. Gill rakers (including rudiments) on first gill arch 14 (large paratype only).

Head length 2.77 (2.22–2.80); depth of body 3.64 (3.69–3.50); snout to anus 1.59 (1.60–1.61); snout to origin of pelvic fins 2.72 (2.77–2.74); snout to origin of dorsal fin 2.86 (2.51–2.95); length of dorsal fin base 2.06 (2.09–1.95); length of anal fin base 3.54 (3.76–3.76)—all in standard length.

Width of body at gill opening 2.34 (3.12–2.64); least depth of caudal peduncle 1.92 (2.62–2.04); snout length 3.46 (3.73–3.21); diameter of eye 5.16 (4.20–5.97); width of interorbital 3.64 (4.65–3.59); length of pectoral fin 1.61 (1.87–1.65); length of pelvic fin 2.31 (2.80–2.29); width of mouth (rictus to rictus) 5.39 (5.25–5.98); mid-center of upper lip to rictus 6.13 (5.80–6.15)—all in head length.

Dorsal spines progressively longer, the ninth 3.50 (3.90–3.59) in head length; first dorsal soft ray 2.45 (2.89–2.54) in head length; second anal spine twice as long as first; third anal spine twice as long as second; third anal spine 3.36 (3.72–3.32) in head length; first anal soft ray 2.29 (2.80–2.56) in head length. Caudal fin slightly rounded.

A pair of large curved canine teeth in upper jaw, each nearly a pupil diameter in length and separated by a distance about equal to the diameter of one of the teeth at the base. A similar pair of canine teeth in lower jaw, lateral to but nearly touching upper teeth when mouth is closed. Remaining teeth small, except one at angle of jaw, those at the symphysis of upper jaw in numerous close-set rows, forming a semicircular mass between the two canine teeth.

Color in alcohol: posterior half of body and caudal fin black except upper and lower edges of caudal fin and dorsal edge of caudal peduncle which are white (magenta in life); anterior half of body light tan (yellow in life) with a median dorsal black band (beginning in a small spot on median upper portion of

upper lip) and a median lateral black band running posteriorly from lower corner of upper lip and tips of lobes of lower lip through eye to merge with black posterior part of body; dorsal and anal fins pale (light blue in life), except for basal part of spinous portion of dorsal fin which is black (this color continuous with that of median dorsal black band) and a narrow horizontal dark line extending from ends of last few dorsal spines posteriorly into the anterior half of the soft portion of the fin about three-fourths the distance from the base of the fin; paired fins pale. The body of the 18.8 mm. juvenile specimen is black except for a broad light-brown band along the back, this band continuing on to top of caudal fin; the remainder of the caudal fin is black like the body except for lower distal corner which is pale; the head is brown with median dorsal and median lateral black bands. In life the band along the dorsal part of the head and body is bright purple. No yellow color is visible on juveniles. The first indication of the yellow coloration is a suffusion of tan over the head and anterior part of the body. This occurs at a length of about 50 mm. (based on estimates of the size of individuals seen underwater).

Labroides phthirophagus is known only from the Hawaiian Islands, where it is a common species. That it escaped being described in Jordan and Evermann's time is probably due mainly to its small size. It is too small to be caught in the usual fish traps or hook and line. An indication of its abundance is its listing [as *L. dimidiatus* by Brock (1954: 307)] among the species consistently tabulated in his underwater transects of Hawaiian reef fishes.

The record of *Labroides dimidiatus* by Günther (1881: 243) from the Hawaiian Islands is open to question. It seems possible that he might have obtained *L. phthirophagus* and confused it with *L. dimidiatus*, for the latter, if it occurs in Hawaii at all, is certainly rare. On one occasion I observed a small individual of what I believe to be this species underwater in Kaneohe Bay, Oahu.

Although generally seen around rock or coral, *Labroides phthirophagus* does not appear restricted to any special habitat. I have observed it in clear water of high coral cover such as Kealakekua Bay and turbid, at times brackish, water lacking living coral such as the Ala Wai Yacht Basin, Honolulu (it is, however, uncommon in the latter area). It occurs in water at least as shallow as 2 feet and has been seen at a depth as great as 90 feet (it may occur deeper—there have been few observations beyond 90 feet).

L. phthirophagus (Greek: *phtheiros*, louse; *phagous*, eat) is named for its habit of feeding on external parasites of fishes.

The food habits of *L. phthirophagus* were suspected from observation of its picking at the surface of other fishes (Fig. 6) and from the knowledge that *L. dimidiatus* feeds on parasitic copepods and isopods from fishes.

In order to obtain more positive evidence of such a mode of feeding, the contents of the alimentary tract of 11 specimens of *L. phthirophagus* in the collection of the University of Hawaii were examined. None of the specimens represent type material. They were

FIG. 6. *Labroides phthirophagus* picking at the body of a goatfish, *Parupeneus multifasciatus*. Reproduced from 16 mm. movie film taken off Manana Island, Oahu.

collected with rotenone from the islands of Oahu, Molokai, Maui, and Hawaii. The results of the examination of the gut contents of these specimens are given below in Table 1, along with the date of collection and the standard length and sex of the specimens.

It seems evident from Table 1 that *L. phthirophagus* feeds primarily on parasitic copepods and isopods from fishes. The fish scales and fragment of fin membrane were probably accidentally ingested in the process of picking at parasites. The cyclopoid copepods (lichomolgids and harpacticoids) do not appear parasitic. They are tiny, and when present in the gut, they are usually numerous, suggesting that they may have been encountered by the labrid in a convenient concentration. That parasites are not the sole diet was further shown by the following observation in Kealakekua Bay, Hawaii. Several nests of the pomacentrid fish *Abudefduf abdominalis* (Quoy and Gaimard) were seen at a depth of 90 feet. When the guarding adult was frightened from one of the nests, a number of other fishes commenced to feed avidly on the eggs, among them an adult *L. phthirophagus*.

Like *Labroides dimidiatus* and *L. bicolor*, *L. phthirophagus* is nonspecific in the fishes which it "services." Among the groups of reef fishes commonly seen participating in symbiotic relationship with *L. phthirophagus* are acanthurids, pomacentrids, scarids, labrids, chaetodontids, mullids, and plectognaths.

Species of *Caranx* are not abundant in the Hawaiian Islands and none were observed in association with *L. phthirophagus*. Only one carangid, *Decapterus pinnulatus* (Eydoux and Souleyet), was seen to associate with the labrid. As a school of this species swam over the bottom off Waikiki, Oahu, a single *Labroides phthirophagus* swam upward to the school. One of the carangids left the school, swam slowly in a small circle, and quivered slightly as the *Labroides* pecked at its body surface.

On one occasion when a *Labroides* was tending a large butterfly fish of the species *Chaetodon lunula* (Lacépède), the latter ceased its gill movements and elevated its operculum. The labrid inserted the anterior half of its body into the gill cavity through the gill opening, where, for several seconds, it presumably searched for parasites.[2] The same behavior was observed for the goatfish *Parupeneus prophyreus* (Jenkins). With the use of self-contained breathing apparatus in clear water of about 40 feet in depth off Manana Island (Rabbit Island), Oahu, an individual *Labroides phthirophagus* was seen to enter the buccal cavity of an adult goatfish, *Mulloidichthys samoensis* (Günther), by way of the mouth, such that the majority of the body of the labrid was lost from view. About five seconds elapsed before the *Labroides* emerged.

Frequently the act of removal of parasites by *Labroides phthirophagus* occurs beneath a ledge or in an interstice in the reef, making observation difficult. Furthermore, the approach of a swimmer usually interrupts the proceedings. For these reasons an effort was made to bring living specimens of *Labroides* into large aquaria where it was hoped detailed observations of behavior could be made.

A total of three were caught underwater with dip nets in Kaneohe Bay and brought to the Honolulu Aquarium. None were maintained in the aquaria long enough for normal feeding behavior to manifest itself; however the reactions of the resident fishes of the aquaria bear mentioning. When placed in a tank containing many moorish idols (*Zanclus cornutus* (Linnaeus)), one balistid (*Rhinecanthus aculeatus* (Linnaeus)), and an unidentified large scorpaenid, the *Labroides* swam about the aquarium, paying little attention to the other fishes. It was evident, however, that the

[2] I suspect that the parasites removed from the gill cavity by *Labroides* are still principally calagoid copepods. In a study of the parasites of the surgeon fish *Acanthurus triostegus sandvicensis* Streets (MS data), I observed individuals of the most common parasitic copepod of this fish, an undescribed species of *Lepeophtheirus*, freely enter and leave the gill and buccal cavities of the fish. The genus *Lepeophtheirus* is the most abundant of the calagoids listed in Table 1.

TABLE 1
GUT CONTENTS OF SPECIMENS OF *Labroides phthirophagus*

DATE COLLECTED	STANDARD LENGTH (MM.)	SEX	GUT CONTENTS
Apr. 10, '50	58	F(ripe)	2 calagoid copepods, 4 larval gnathiid isopods, fish scales
Sept. 21, '51	53	F	4 calagoid copepods, 25 harpacticoid copepods*
May 11, '52	60	F	3 calagoid copepods, 1 lernaeid copepod†, 88 lichomolgid copepods‡
Dec. 31, '52	42	M	2 calagoid copepods, 1 lernaeid copepod†
	49	F	14 calagoid copepods, 1 lernaeid copepod†, 4 larval gnathiid isopods
	55	F	10 calagoid copepods, 1 lernaeid copepod†, 6 larval gnathiid isopods, fragment of fin membrane
	76	M	2 calagoid copepods, 14 digenetic trematodes§
Jan. 21, '53	39	F?	1 calagoid copepod, 8 larval gnathiid isopods
June 19, '53	60	F	1 calagoid copepod, 19 harpacticoid copepods*
July 25, '55	58	F	6 calagoid copepods, fish scales
Aug. 7, '55	63	F	14 calagoid copepods

* *Tisbe* sp.; most species are free-living but at least one is commensal (in a pelecypod).
† *Penicalus* sp., generally attached to fins.
‡ Many members of this family of cyclopoid copepods live commensally with tunicates, pelecypods, flatworms, etc.; however, according to Dr. Paul L. Illg, this species of copepod does not fit well into any genus so far proposed. Although no lichomolgid has turned up as parasitic on a vertebrate, this one is sufficiently distinctive anatomically (the arrangement of the maxillary suggests its use as a substitute masticatory appendage) that it might have developed a divergent feeding mechanism.
§ Undigested, probably a gut parasite of the *Labroides*.

moorish idols and the trigger fish were immediately aware of the new arrival, for they reacted as in the normal environment. As the *Labroides* swam past individual fish, many were observed to cease swimming, and occasional moorish idols stopped their respiratory movements and raised their gill covers. The following morning the *Labroides* could not be found in the aquarium.

The second *Labroides* was added to a tank containing two parrot fishes (*Scarus* sp.) about 250 mm. in length and seven surgeon fishes (*Acanthurus* spp.). Again the *Labroides* paid little heed to the other fishes, but they reacted characteristically. The surgeon fishes swam about nervously in a restricted area of the tank. The behavior of the parrot fish was almost ludicrous. They followed the *Labroides* around the aquarium, stopping occasionally to literally stand on their tails, waggle their pectoral fins, and seemingly to ogle the labrid, as if to entreat it to perform the expected services. The parrot fishes and surgeon fishes were recognized as ones which had been in the aquarium at least several months. This poses a question which is as yet unanswered. Do these fishes learn the role of *Labroides* through experience or is their behavior innate? The answer could be provided through observation of *Labroides phthirophagus* with aquarium-reared fishes or with fishes taken from an area where species of *Labroides* are known not to occur. If learned through experience, how long is the capacity for symbiotic association retained?

The second *Labroides* was left overnight in the aquarium, and it also was gone the next day. It is not known whether this and the first *Labroides* which disappeared were eaten by fish or whether they escaped down the drains (which, it was later noted, were not screened).

The third *Labroides* was placed in an aquarium containing only adult wrasses of many species. It was immediately chased about the tank by several individuals of different species and ultimately eaten by one of them. This was totally unexpected, for various wrasses were among the fishes which were observed being serviced by *Labroides phthirophagus* in the reef environment. The immediate

pursuit of the *Labroides* in the aquarium suggests that the wrasses might have been conditioned to rapid seizure of food items added to the surface of the tank, and that this reaction may have superseded the one which would occur in the normal habitat.

When in the proximity of other fishes, *Labroides phthirophagus* exhibits the same unusual oscillatory mode of swimming as seen in *L. dimidiatus*, although not as commonly.

As previously mentioned, the act of removal of ectoparasites by *L. phthirophagus* frequently takes place in a region of cover such as beneath a ledge. Repeated observations of one such ledge at Manana Island, Oahu, revealed that a pair of this species of *Labroides* could invariably be found at or near this site. These observations continued for a period of over three years. Other pairs or groups of three fish were similarly checked over long periods of time at the following locations: Waikiki, Kaneohe Bay, Hanauma Bay, and Kealakekua Bay, Hawaii. I conclude from these and lesser observations that adult *L. phthirophagus* tend to remain in a restricted area of the reef.

As with *Labroides dimidiatus*, it is believed that fishes seek out the area where *Labroides phthirophagus* occur in order to have their parasites removed. The first evidence that fishes might come to a *Labroides* site from beyond the immediate vicinity was the sighting at Manana Island of an adult manini, *Acanthurus triostegus sandvicensis* Streets, swimming from at least 40 feet away direct to the *Labroides* ledge where it stopped and erected its fins. As one of the *Labroides* swam up to this fish, the latter was speared and taken ashore. Macroscopic examination revealed the presence of three calagoid copepods. Seemingly purposeful swimming by other fishes to *Labroides* areas has been observed. Generally there is a concentration of reef fishes around a *Labroides* site. I have on several occasions located such a site by first noting a greater density of reef fishes in a restricted area than could be explained by any other reason.

Labroides sites are usually well separated from one another. This first became evident around the patch reefs in Kaneohe Bay. *Labroides phthirophagus* is generally found at a depth of about 5 to 20 feet at the steep margins of these reefs rather than their shallow, truncate tops. The spacing between sites, at times remarkably regular, is now linear and more readily perceived by an observer swimming around such a reef.

Although occurring singly or in groups of as many as five individuals, *Labroides phthirophagus* is most commonly seen in pairs. Often groups of three or more contain one or more juveniles in the company of a pair of adults. When a pair of adults is seen, it is natural to expect that one would be a male and the other a female. There is some evidence that this is the case. Of the four specimens shown in Table 1 which were collected at a poison station on December 31, 1952, two are males and two are females. One of the two paratypes which were speared on October 14, 1955, at Waianae, Oahu, is a ripe female (standard length 64 mm.; length of ovary *in situ* 12 mm.) and the other appears to be a male. These two fishes were found together and were the only two seen in the area surveyed.

Labroides rubrolabiatus, new species
Pl. 1 B

HOLOTYPE: U. S. Natl. Mus. No. 164603, a female specimen, 54 mm. in standard length and 66.5 mm. in total length, collected by J. Randall with rotenone in the lagoon at a depth of 20 feet next to a large coral head about 100 feet from shore one-fourth of a mile east of the entrance to Papetoai Bay, Moorea, Society Islands, on May 3, 1956.

PARATYPES: U. S. Natl. Mus. No. 164604, a female specimen, 51 mm. in standard length, collected by J. Randall with a spear 30 feet off the lee reef near the boat entrance of Caroline Atoll (10° S. 150° 14′ W.) at a depth of about 15 feet on February 12, 1956; Stanford Univ.

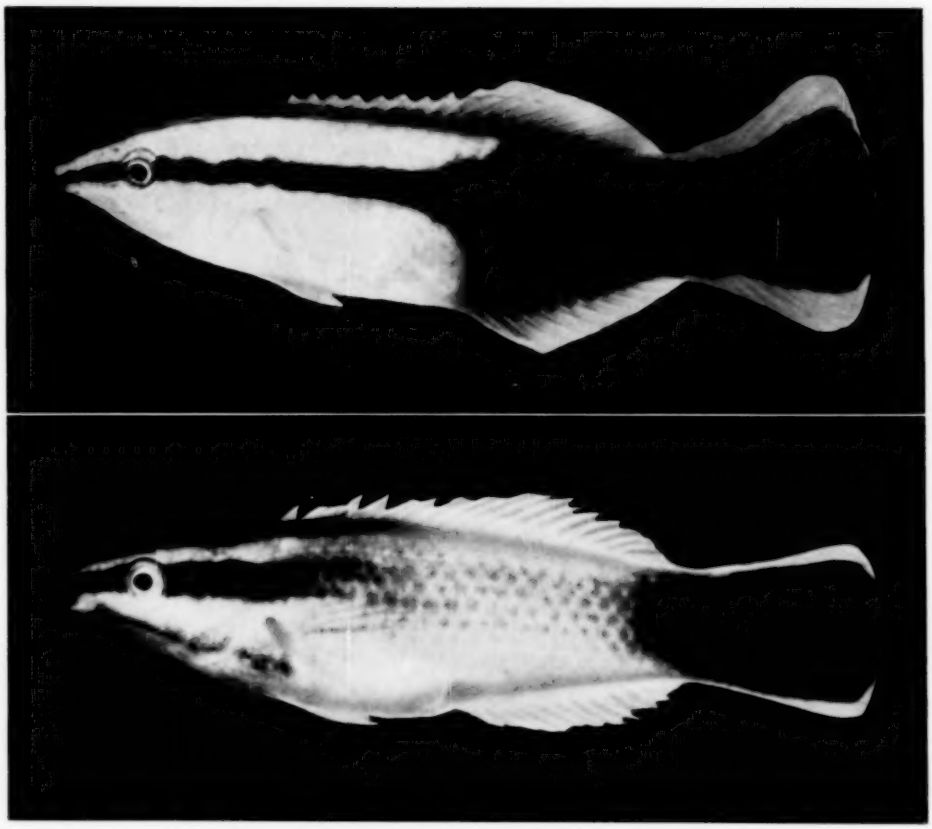

Plate 1

A. *Labroides phthirophagus*. Holotype, Oahu, Hawaiian Islands. Standard length, 68 mm.
B. *Labroides rubrolabiatus*. Holotype, Moorea, Society Islands. Standard length, 54 mm.

Mus. No. 48871, a female specimen, 48 mm. in standard length, collected by J. Randall with a spear in the Moorea lagoon just east of Tareu pass at a depth of 8 feet on May 22, 1956 (specimen was picking on the body of a female *Scarus sordidus* Forskål when speared); British Mus. No. 1956.8.14.1, a female specimen with mature gonad, 45 mm. in standard length, collected with a spear by J. Randall within 75 feet of the locality of the May 22 specimen at a depth of about 10 feet on March 29, 1956.

Two more specimens collected by the author, a male 46.5 mm. in standard length, from a depth of 7 feet in the Moorea lagoon near the entrance to Papetoai Bay on July 1, 1956, and a 54.5 mm. female from 15 feet in the pass at Takaroa, Tuamotu Archipelago, Nov. 9, 1956, have been placed in the collection of the University of Hawaii. Both specimens were speared, the former as it was picking at the dorsal fin of *Zebrasoma scopas* (Cuvier). No external differences could be ascertained between the one male specimen and the female specimens.

Some proportional measurements of the paratypes were difficult to make because of injury from spears.

DESCRIPTION: Based on the holotype and the smallest (45 mm. in standard length, 55.3 mm. in total length) and the largest (51 mm. in standard length, 62.5 mm. in total length) paratypes. Measurements are recorded for the holotype, followed in parentheses by data for the small and large paratypes, respectively. Meristic data are the same for the holotype and paratypes (with the possible exception of median predorsal scales which are obscure and difficult to count), hence only a single number is given for each count.

Dorsal fin rays IX, 11; anal fin rays III, 10; pectoral fin rays 13 (the uppermost rudimentary, the next unbranched); pelvic fin rays I, 5; principal caudal rays 14. Lateral line scales 28, the last enlarged and bearing a prominent lateral line tube (scales extend posterior to lateral line nearly half the remaining length of caudal fin); scale rows above lateral line to base of first soft dorsal rays 3 (the upper row extending on to base of dorsal fin); scale rows below lateral line to base of first anal soft rays 8 (two additional rows of moderately large scales on base of anal fin at this point); median predorsal scales 8 or 9; snout, chin, throat, and dorsal part of head naked. Gill rakers (including rudiments) on first gill arch of 48 mm. paratype 15.

Head length 2.78 (2.67–2.77); depth of body 3.48 (3.50–3.69); snout to anus 1.66 (1.70–1.69); snout to origin of pelvic fins 2.70 (2.59–2.66); snout to origin of dorsal fin 2.92 (2.74–2.91); length of dorsal fin base 1.99 (2.08–2.07); length of anal fin base 3.60 (3.89–3.90)—all in standard length.

Width of body at gill opening 2.70 (2.81–2.75); least depth of caudal peduncle 2.16 (2.33–2.32); snout length 2.85 (2.91–2.87); diameter of eye 5.11 (4.82–4.98); width of interorbital 3.81 (4.02–3.88); length of pectoral fin 1.50 (1.53 and 1.53); length of pelvic fin 1.96 (1.96–1.94)—all in head length.

First dorsal spine 8.64 (9.62–9.20) in head length; dorsal spines progressively longer (filaments of interspinous membranes extend beyond spine tips), the ninth 3.40 (3.75–3.58) in head length; first dorsal soft ray 2.43 (2.42–2.52) in head length; first anal spine nearly half as long as second; second anal spine about two-thirds as long as third; third anal spine 3.63 (3.47–3.57) in head length; first anal soft ray 2.18 (2.00–2.11) in head length. Caudal fin slightly rounded.

Width of mouth (rictus to rictus) equal to eye diameter. Center of upper lip to rictus about 5 in length of head. Distance between lobes of lower lip about one-third diameter of eye.

A pair of curved canine teeth (the uppers more curved than the lowers) anteriorly in each jaw, about one-fourth eye diameter in length. Upper canines fit inside lowers when jaws are closed (upper and lower canines on one side separated by a distance slightly less than diameter of base of one of the teeth). A

large semicircular mass of fused teeth in center of upper jaw just posterior to upper canines. This mass is as long as the upper canines with which it is in contact basally. It is indented anterocentrally. An inconspicuous band of small teeth may be seen anteriorly in the lower jaw. A canine tooth at angle of jaw.

Color in alcohol of Moorea specimens: light greenish brown, shading anteriorly on head to light bluish gray, with a black band running from mouth through eye on to body; on the body the band broadens as it passes posteriorly and becomes progressively indistinct until, in the median part of the body beyond the tip of the outstretched pectoral fin, it is barely discernible or absent; posteriorly it reappears, becoming black on caudal peduncle and caudal fin (which is completely black except for upper and lower edges and the posterior rounded corners which are white); a broad black middorsal band runs posteriorly from tip of snout and gradually lightens until it disappears at rear base of spinous portion of dorsal fin; a diagonal dusky streak from chin across cheek below eye to lower base of pectoral fin (obscure in 45 mm. paratype); spinous portion of dorsal fin dusky basally, pale distally; anal fin and soft portion of dorsal fin pale with a dark horizontal streak anteriorly located about two-thirds the distance from base to margin of fins; paired fins pale except for dark edges of pectoral fin rays.

The following color note from life was made of the holotype: body from region of end of pectoral fin to caudal peduncle orange; caudal peduncle and caudal fin (except for upper and lower edges which are pale-blue violet) jet black; a black band passing from snout through eye, broadening on to anterior portion of body and merging gradually with dusky orange on median part of body; a similar black band from snout to anterior third of back where it also merges with the orange; a narrow blackish line from slightly ventral and posterior to rictus to lower base of pectoral fin; narrow band on head between midlateral and middorsal bands chartreuse; head below midlateral band chartreuse, shading to pale blue ventrally; lips edged in bright red; abdomen pale blue shading to dull pale yellow posteriorly; dorsal fin orange basally, hyaline distally (only tips of interspinous membranes are hyaline whereas the outer half of the soft portion of the fin is clear); anal fin divisible by color into three lengthwise bands, light blue basally, orange in the middle, and hyaline distally; paired fins pale except for dark edges of pectoral rays.

The brightness of the life color of the holotype had already faded when the photograph of Plate 1 was taken. The orange of the body and especially the yellow green of the head were more brilliant when the fish was alive.

The specimen from Caroline Atoll, although exhibiting the same general color in alcohol, is more melanistic than the ones from Moorea. The median portion of the body is dusky, almost blackish, and the white margins of the caudal fin are narrower and restricted to the outer half of the fin.

The life colors were approximately the same. The color on the head was noted in life as dusky iridescent green; the middle of the body was dusky orange and the abdomen dusky yellow; the narrow band on the cheek was blackish orange; the edges of the caudal fin were hyaline violet; the lower lip was bright red and the upper mottled with red; the dorsal and anal fins were orange basally and hyaline distally, and the paired fins pale with a purplish hue.

One pair of *L. rubrolabiatus* at Caroline Atoll was seen in company with a juvenile which was iridescent blue with a broad midlateral black band. One of another pair showed intermediate coloration—the anterior half was bright blue with the black median band, and an orange-brown area was just appearing in the middle of the body.

L. rubrolabiatus is the smallest of the four species of *Labroides*. Individuals seen underwater rarely appear even slightly larger than the largest specimens collected. An excep-

tionally large one, estimated at between 60 and 70 mm. in standard length, was sighted on the top of a patch reef in the lagoon at Takaroa.

This species was first seen by me during a short stay at Caroline Atoll. It was abundant in the clear water off the lee reef, but was not seen in the lagoon (which lacks a pass). It was often seen in pairs, and commonly two of the little labrids picked rapidly over the body of a larger fish simultaneously, paying special heed to the head. Only a slight tendency toward the oscillatory swimming as described for *L. dimidiatus* was noted. It was seen to peck at the bodies of numerous parrot fishes (*Scarus* spp.) and surgeon fishes (*Ctenochaetus striatus* and *Acanthurus* spp.), the groupers *Cephalopholis argus* Bloch and Schneider, and *Plectropomus leopardus* (Lacépède) (3½ feet in length), the giant wrasse *Cheilinus undulatus* Rüppell (about 4 feet in length), the goatfish *Parupeneus chryserydros* (Lacépède), and the lutjanoid *Monotaxis grandoculis* (Forskål). Later at Tahiti and Moorea the list of species seen in association with *Labroides rubrolabiatus* was extended such that it encompassed nearly all the families of reef fishes in the area.

L. rubrolabiatus has been observed entering the gill cavities of parrot fishes. This was first seen at the entrance to the pass of the atoll of Takaroa in the Tuamotus. The labrid inserted the anterior half of its body through the gill opening of *Scarus harid* Forskål. The second observation was made just outside the barrier reef on the southeast coast of Moorea at a depth of 10 feet. About a 40 mm. *Labroides* was seen to pick several times at the right gill opening of *Scarus vermiculatus* approximately 250 mm. in standard length. The parrot fish angled its left side downward and elevated its gill covers. The labrid slipped into the gill chamber and was completely lost from view for about two seconds. On two occasions outside the reef at Takaroa *L. rubrolabiatus* was seen to enter the buccal cavity of adult groupers of the species *Epinephelus fuscoguttatus* (Rüppell) via the mouth.

The stomach of the paratype from Caroline Atoll was opened and found to contain one larval gnathiid isopod. The 45 mm. paratype from Moorea was similarly examined; this fish had eaten nine larval gnathiid isopods.

In the Society Islands and Tuamotus the species is not as common as *L. dimidiatus* or *L. bicolor*. It occurs outside the reef and in lagoons, usually at depths greater than 15 feet, and in areas of good circulation with much live coral and clear water.

At the atoll of Tikahau, Tuamotu Archipelago, outside the reef just north of the pass, *L. rubrolabiatus* was seen at a depth of 120 feet, in the company of a single *L. dimidiatus*. No specimens were collected from Tikahau or from Nuku Hiva in the Marquesas, where the species was also observed underwater.

Whether the species will be found to be restricted to southeast Oceania or whether it will eventually be taken farther to the west remains for further collections to reveal.

The species is named *rubrolabiatus* (Latin *rubro*, combining form of *ruber*, red; *labiatus*, lipped) in reference to the color of the lips in life.

ACKNOWLEDGMENTS

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Metamorphosis of the Shell in the California Sea Hare, *Aplysia californica* Cooper

LINDSAY R. WINKLER[1]

DESPITE ATTEMPTS by Carazzi (1905), Mazzarelli (1893), Saunders and Poole (1910), and the present writer, the metamorphosis of *Aplysia* has not yet been observed, nor has it been possible to follow through the changes in the shell which take place as the animal metamorphoses from a planktonic veliger to a sluglike sea hare. This is because the veliger shell is lost sometime during metamorphosis so that the evidence of metamorphosis in the animal becomes obscured. In one case only has the writer seen a small outmoded veliger shell hanging in place by a very thin membrane in the apexial concavity of a very young specimen from a new species obtained from the Gulf of California.

However, the neaplysiids which are known only from the west coast of North America are distinct in that they possess a special attachment plate extending from the inner apexial area. This plate contains the built-in veliger and the metamorphic shell. This is best seen in young shells, as older animals tend to strengthen their shells by overlaying with added shell material.

MATERIALS AND METHODS

The shells of *Aplysia californica* Cooper, two to five inches in length, were procured from newly sacrificed young animals. The shells were preserved in 70 per cent alcohol. Study was done under a dissecting microscope.

EXPERIMENTAL DATA

The position of the metamorphic shell is indicated in Figure 1. The portion of this shell outline which normally comprises the veliger shell at hatching may be approximated by comparing the shell of laboratory incubated egg strings at the time of hatching with the inner areas of the shell nucleus. Size measurements are helpful in determining the areas involved in the prehatching shell. The size of the veliger from top of the hood is approximately 150 μ.

The angle of the hood in relation to the base of the shell at the time of hatching (Fig. 2), compared to the corresponding dimension in the shell nucleus, indicates the approximate starting point of free-living existence. The end of the pelagic period probably occurred at the time of the first major change in shell character in the area built after the initiation of free-living existence.

In many specimens the shell built between the time of hatching and this supposed end of the pelagic period is of slightly different color. It is a less transparent yellow and has fine growth lines, perhaps reflecting the change from the prehatching yolk food to the food that may have been available to it in the free-swimming state.

An examination of the veliger shell (Fig. 2) shows that the tendency to build a spiral shell is already indicated at time of hatching by the asymmetrically thickened edge of the initial spire. The tendency to spiral rapidly increases during the early postveliger existence. The writer believes that this is a crawling stage in which the snail's foot has taken over the locomotion for which it was not yet prepared at the time of hatching. This early stage, though very different from the adult, is probably very gastropodlike, with the animal crawling on its foot and feeding upon microscopic algal forms but retracting within its spiral shell which it closes with its operculum. This constitutes the first stage of metamorphosis.

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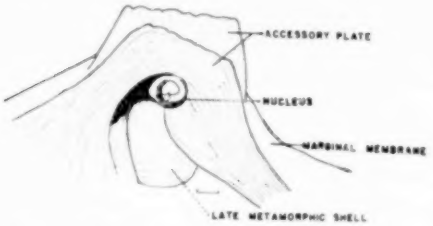

FIG. 1. Nucleat area of a shell of *Aplysia californica* Cooper showing the stages of development from the microscopic free swimming veliger to the adult plan of shell construction. The measure indicates 150 μ.

FIG. 2. Two views of newly hatched veliger larva. The measure indicates 150 μ.

As the shell completes its first convolution, it starts an even more marked tendency to flare out and flatten to form a covering over the animal rather than a house into which it may retract. At the end of the first whorl this tendency has become dominant, and by the end of the further half whorl the shell has opened out into a spoon-shaped covering which is indicated as the late metamorphic shell in Figure 1. Mazzarelli (1893) pictured a metamorphic animal which is probably a somewhat later form than this, carrying its outgrown shell on its back. During the metamorphosis, additional material is laid down on the shell, in which process the nucleus is probably first a point of muscle attachment. However, in *A. californica* an auxiliary plate is soon formed, paralleling the curvature of the intermediate metamorphic shell, which, along with later modifications, forms a new post-metamorphic plan of growth. This neaplysiid plate forms on a plane with the embryonic nucleus and becomes an extension of it.

The entire outline of the shell is modified after metamorphosis, the original larval shell being used only as a building block in the future adult shell. These shell changes are indicated in Figure 1 by the lines of growth.

SUMMARY

1. The shell nucleus, containing the veliger shell, is present in adults of *Aplysia californica* Cooper as a building block in the auxiliary plate characteristic of this subgenus.

2. The metamorphic forms of the shell are clearly preserved.

3. The implications of this shell metamorphosis are (a) a short swimming stage, (b) an intermediate, gastropodlike crawling stage in which the shell is a place of retreat, (c) a metamorphic stage with a spoon-shaped shell by which the animal is covered, and (d) a late metamorphic stage in which the animal outgrows the shell, which becomes vestigeal in the adult animal.

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Specific Characters and Character Variants in Adults and Larvae of the Genus *Paratrombium* Bruyant 1910 (Acari, Trombidiidae), with Descriptions of Two New Species from Western North America

IRWIN M. NEWELL[1]

THE GENUS *Paratrombium* was established by Bruyant for a larval mite, which he named *P. egregium*, found in a vial containing Diptera, Coleoptera, and possibly other insects. The outstanding characteristics of this larva as indicated in the drawings provided by Bruyant were: (1) the large postscutal dorsal plate, (2) the characteristically striate anterior portion of the scutum, (3) the form and orientation of the heavy, sharp prosensillar setae which appear to arise from the end of long canals, (4) the swollen, bilobed tip of the rostrum, (5) the elongate, pectinate tritorostral setae, (6) the heavy rakelike inner setae of coxae I, (7) the presence of a single pair of intercoxal setae, (8) the number (four) and orientation of the setae between coxae III and the anus, (9) the presence of only two scythe-shaped claws on tarsus III. In all of these features, the species described by Bruyant resembled so closely the one described below as *Paratrombium bidactylus* n. sp. as to indicate that these are congeneric.

It should be pointed out that the original description of *P. egregium* differs from *P. bidactylus* n. sp. in three important respects: (1) the presence of a pair of slender, elongate setae between the sensilla and prosensillar setae of the scutum, (2) a coxal setal formula in the larva of 2-1-1 compared with 2-2-1 in *P. bidactylus*, and (3) the possible absence of the four characteristic elongate setae at the posterior margin of the body. The first of these apparent differences is based on an artifact; for the transverse suture which partially divides the scutum into anterior and posterior portions appears so sharp and delicate that Bruyant unquestionably mistook it for a fine seta. With regard to the second of these characters it should be pointed out that Oudemans (1910) represented this species as having two setae on each of coxae II of the larva; and moreover showed only four pairs of setae on the scutum, including the single pair of sensilla. Oudemans' somewhat more detailed figures were apparently prepared from Bruyant's own material, hence, the original description of *P. egregium* was in error on this point also. With regard to the third point mentioned above, neither Bruyant nor Oudemans showed the characteristic setae at the posterior end of the hysterosoma which are found in the larvae of *P. bidactylus*. It should be pointed out, however, that the writer's drawings have been made from unengorged larvae while those drawn by Bruyant and Oudemans were of engorged larvae. Both Bruyant and Oudemans showed a total of 28 postscutal and postcoxal setae whereas in *P. bidactylus* there are 30. This could be a true specific difference or it might possibly be due to the loss of one of the pairs of setae during the period of feeding in the specimens from which the available figures of *P. egregium* were drawn. At any rate, the close morphological similarity between *P. egregium* and the two species described below as *P. bidactylus* n. sp. and *P. quadriseta* n. sp. is so close as to indicate beyond reasonable doubt that they are congeneric.

The differences between the two larvae described below appear to be adequate to indicate that two distinct species are involved, and since they were obtained from known adult females, it is possible to determine what adult characters, if any, show variations of a

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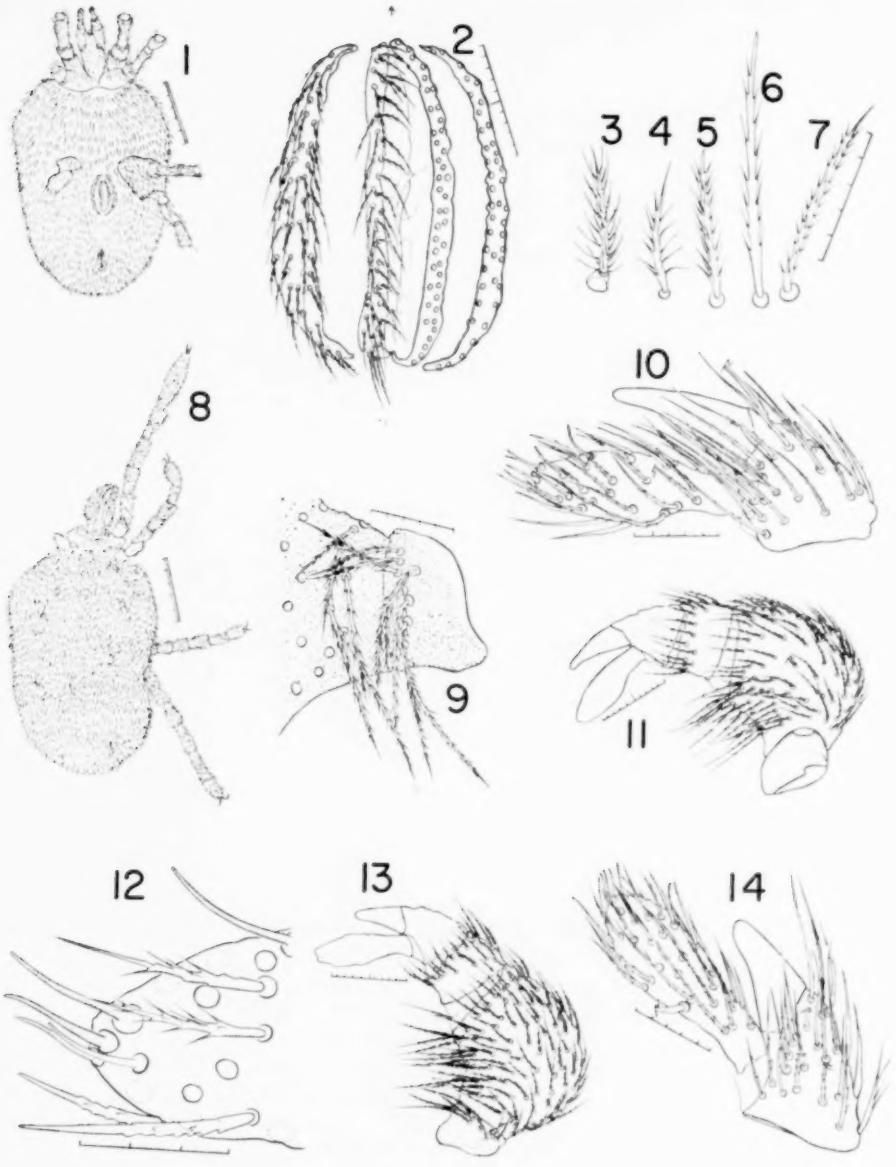
possible specific nature. Correlations between larvae and adults in this group are much needed, because the two instars are often collected under quite different circumstances, with the adults coming from general collections, and the larvae often being found on their insect hosts. Because of the great change in form which accompanies the transformation from larva to nymph and nymph to adult in the Parasitengona, it is impossible to correlate larvae and adults with certainty by any means other than rearing.

There are even more compelling reasons, however, for establishing correlations between larvae and adults. In the first place, adults within a given genus of the Parasitengona are separated from each other by characteristics largely of a relative nature. The intraspecific variation in the adults of these mites is so great that it has not yet been adequately analyzed for any single species within the entire group. At the same time, *interspecific* differences are relatively small, so that in examining two adult specimens within a given genus, which show moderate differences, there is always the question of whether these differences are of a specific nature, or whether they fall within the range of variation of a single species. The primary difficulty here is that the chaetotactic differences which are of such great value in separating orthotrichous forms are almost totally unavailable in the highly neotrichous Parasitengona. With intensive study of the chaetotaxy of adults, exceptions to this are slowly coming to light, but they are at the present time very few in number, and it appears increasingly likely that there are certain genera in which absolute chaetotactic differences will never be of great importance in differentiating species. While it is to be hoped that it will never be necessary to have *both* larvae and adults in order to provide positive determinations of species, there is no assurance at this time, in the present inadequate state of our descriptive accounts of the adults of these species, that such will not be the case. Old species must be carefully redescribed, and new species must be described in considerably greater detail and with far greater accuracy than they have been in the past if we are to progress in knowledge of the adults as far as we have in knowledge of the larvae.

In the second place, correlations between larvae and adults are necessary in order to provide additional information upon which to determine relationships within the Parasitengona. In very many cases, the best generic characters are found within the larvae, and in any case it is always well to have the larval characters in addition to the adult characters in arriving at conclusions concerning relationship. Here again, it should be pointed out that even recent descriptions of larvae of Parasitengona are inadequate from a morphological and systematic standpoint. All too often, for example, the chaetotaxy of the palpi is presented in a very sketchy manner, if at all, and the segments of the legs, despite their greater size, come out only slightly better. At the species level, detailed studies of the larvae of closely related species are desirable in order to substantiate the validity of minor differences suspected of having specific value in the adults. For example, in the present case, there are a few very minor differences between the adults of *Paratrombium bidactylus* and *P. quadriseta*. If one had only the adults of these two species, there would be considerable doubt whether the differences in eupathidial counts on the palpal tarsus, the slight difference in the posterior end of the crista metopica, the chaetotaxy of the anterior portion of the scutum, and the number of setae on genital and paragenital sclerites were of real specific value. It is still possible that studies of additional adults will show these characters to intergrade at least in part. Yet the studies of the larvae show clearly enough that we have two distinct species, hence any differences found between adults of these two species are of possible specific value, and are worth investigating in detail.

In the present paper, the terminology uti-



FIGS. 1-14. *Paratrombium bidactylus* n. sp., female: 1, venter, female; 2, genital opening; 3, typical seta posterior and lateral to anus; 4, seta from genital sclerites; 5, seta from intercoxal area; 6, seta of coxa II; 7, seta behind the coxa II; 8, dorsum; 9, trochanter of palp, posterior; 10, tibia and tarsus of palp, anterior; 11, entire palp, anterior, chaetotaxy of tibia and tarsus omitted; 12, tip of palp, posterior; 13, entire palp, posterior; 14, tibia and tarsus of palp, posterior.

lized in the earlier work on the Johnstonianidae (Newell, 1957) has been followed, as has the convention for designation of the positions of setae on the segments of the appendages. The decimal system of notation has been extended to the scutum as well as the appendages. In the case of the scutum, the starting point (0.00) will be the most anterior point on the median line of the scutum. In *Paratrombium* and many other genera, the anterolateral lobes of the scutum actually extend beyond this point, but since these are rather poorly defined in some genera or in particular specimens of many species, it is better to utilize the more readily recognizable point. In general this will be the most anterior point on the median axis of the scutum, regardless of whether or not this is precisely the anterior end of the entire plate.

Attention should be called to the indiscriminate use of the term crista metopica. This term was applied by early authors to the very pronounced ridge which runs longitudinally over the dorsum of the propodosoma of many species of the Parasitengona. It is primarily a strengthening support for the dorsal wall of the propodosoma, and also provides attachment for certain of the muscles of this part of the body. It should be kept in mind that the crista metopica is only one part of a larger sclerite, the scutum, which is of considerably greater significance both structurally and taxonomically than the crista metopica alone. The crista metopica, because it is so much more conspicuous than the scutum (the margins of which are often so faint as to be detectable only in carefully dissected and mounted material), is often described as though it were an isolated structure in itself. In a few of the Parasitengona it does approach this status, especially in some of the larger Erythraeidae in which the scutum is only very slightly broader than the crista. At some points the crista in certain genera may even be the *only* portion of the scutum to be found. However, such cases are extremely rare; and there are few species in which the scutum does not extend at least somewhat beyond the limits of the crista metopica. The neglect of the peripheral portions of the scutum in descriptive accounts is a serious omission. It is also a mistake to extend the term crista metopica to apply to the scutum as a whole. A description of the scutum should be based upon dissected material, or if this is impossible, upon carefully compressed specimens in which all levels of the scutum are lying in approximately the same plane.

The present study was carried out under a research grant (NSF-G1833) from the National Science Foundation to the University of California at Riverside. It was further aided by research grants from the University of California, which supported all of the field work upon which this study was based. The drawings were prepared by Mari Riess of the University of California at Riverside. In these figures, the scales provided are marked off in 10 μ units except for the few marked in 100 μ units. The latter are drawn with a double base line.

PARATROMBIUM Bruyant 1910

ADULT: Trombidiidae of medium to large size, and brilliant red color. Scutum with sensilla in middle one-third of plate, widest portion of scutum at anterior end; crista extending from posterior end of scutum to a group of setae near the most anterior point on the midline of the scutum. Eyes distinctly stalked, two corneae on each side. Dorsal hysterosomal setae all of one type, peripectinate, arising from small, erect, conical papillae. Coxal rings I and II open dorsally, a long slender supracoxal seta on I. Genital and paragenital sclerites both well developed and bearing numerous peripectinate setae; three pairs of genital acetabula. Tarsus of chelicera bearing a row of minute denticles along the upper margin, this row of denticles also continuing down over the side of the basal portion of the tarsus (Figs. 22,

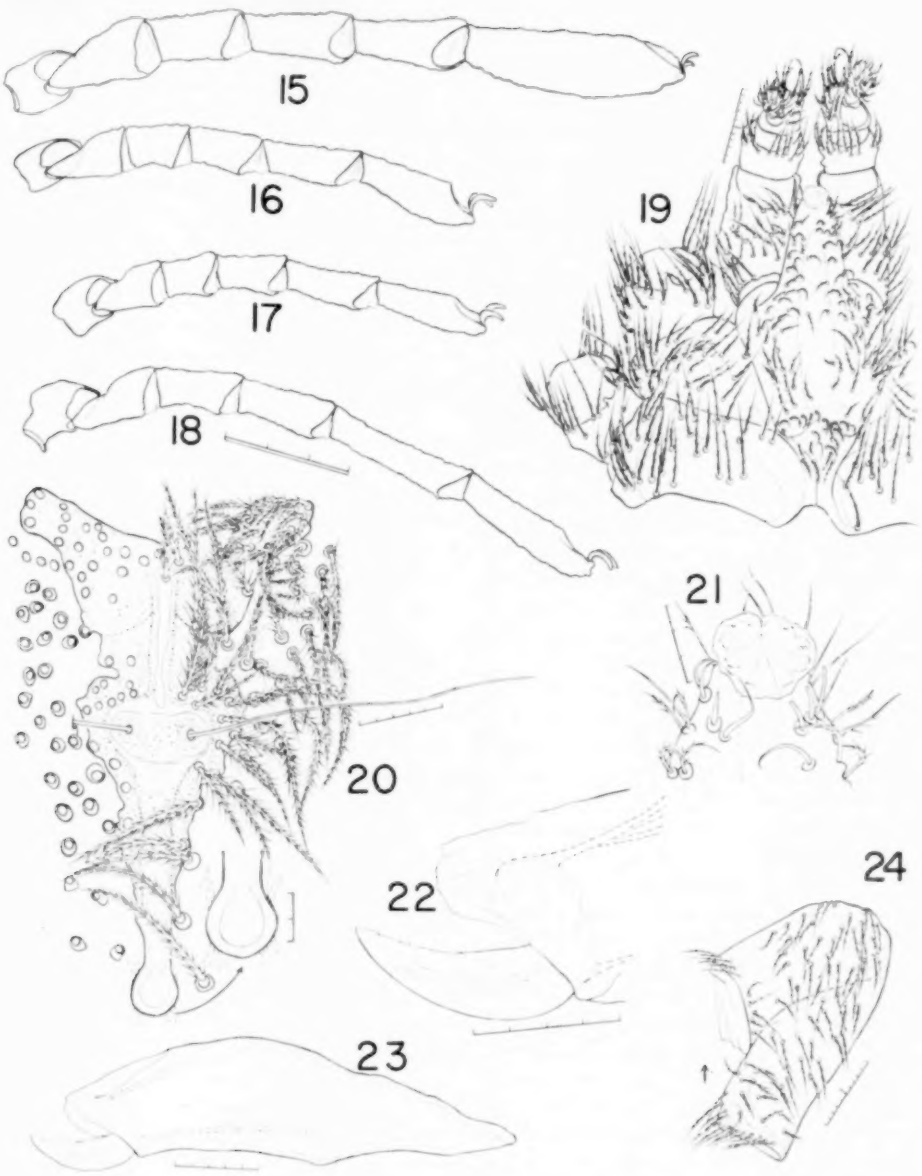
55). Palpi of normal form for family, odontus unidentate, paradont absent. Tibia with no clearly defined ctenidium, but with a group of unusually smooth setae anteroventrally, near the insertion of the tarsus. Tarsus with a single solenidion posteriorly and a variable number of eupathidia.

LARVA: Scutum with four pairs of setae, postscutum with two or four pairs; postscutum nearly as wide as scutum. Coxa I with a slender supracoxal seta and two ventral setae, the medial one of which is greatly enlarged and bears a number of long, fingerlike teeth on the posterior margin. Urstigma very large, concealed under the posterior margin of coxa I in ventral view, visible only by transparency. A single pair of intercoxal setae. *Lassenia*-organ present. Palpi with only four segments visible in ventral view, but trochanter present as a very small plate dorsally on base of palp (Fig. 40). Palpi oriented so that the morphological dorsal line forms the lateral margin of the palp as seen in dorsal or ventral view. Trochanter and patella devoid of setae, femur with a single seta. Tibia with a deeply cleft odontus plus three simple setae; no specialized paradont present. Tarsus reduced to a small hemispherical cap bearing a number of setae of variable size and form, but one of these is strongly scythe-shaped. Rostrum with only the protorostral and tritorostral setae. Basifemur and telofemur of all legs fused. Solenidial formula of patella (2-1-1), of tibia (2-2-0), and of tarsus (1-1-0). Vestigial setae present on patella I and II and tibia I, famulus on tarsi I and II; companion setae absent. Tarsi I and II with three claws each, III with anterior and median claws of same form as on I and II, but with posterior claw reduced to a very short rudiment (at least in the type species and the species described in this paper).

CHARACTERS SHOWING INTERSPECIFIC VARIATIONS IN THE GENUS *Paratrombium*

Although the study of interspecific variation within a genus is of practical value in the identification of species, this should never be regarded as the sole purpose of such studies. Any type of variation observed, whether of practical utility in a key or not, should be investigated as it may indicate relationships within the genus, or evolutionary trends. When combined with similar studies in related genera, they provide information on whether or not the same types of adaptive changes have occurred in different genera. In the large Parasitengona, intensive studies of variation are even more important than in the other genera, because the differences separating species are more often of a purely relative nature; that is, they involve variations of continuous rather than discontinuous types. As a consequence of the studies of the two forms described here, a number of characters were discovered which show variations of possible specific value. These are summarized below, the characters for adult and larva being listed separately. Most of the character variants listed in the tables are self explanatory, but some require further explanation. Most of them show variation of a continuous type. One exception is found in the dorsal chaetotaxy of the larva, in which the postscutum has two setae in one of the species and four in the other. These variants are discontinuous only in the sense that no intergradations between them have been found up to the present time. While it is not inconceivable that these exist, it is interesting to note that the closest approach is found in occasional specimens of *P. bidactylus* in which there are two setae on one-half of the postscutum. Even in these cases, the half of the postscutum in which the duplication has occurred does not resemble its counterpart in *P. quadriseta*, since the placement of the two setae is markedly different.

The variations in form of the hysterosomal setae (character 14, adult) are more or less discontinuous, although it is quite certain that many gradations will be found when the genus is more adequately known. If Feider's assumption (1952) that nearly all species of



FIGS. 15–24. *Paratrombium balactrias*, n. sp., female: 15–18, legs I to IV; 19, gnathosoma and propodosoma, ventral; 20, scutum of dissected female; 21, tip of rostrum, ventral; 22, cheliceral detail; 23, chelicera; 24, coxae III and IV.

the old genus *Dinothrombium* actually belong in *Paratrombium* is correct, the probability of intergradation in setal types is very great.

Nearly all of the characters listed below show variants which are useful in distinguishing the two species under consideration here. It is to be expected that as more species are adequately described even more characters and variants can be added to this list. At the same time, as other populations of the two species involved are studied, the range in variation of the characters will become greater. The variants of the characters are summarized in the form of a formula key. The purpose of such a key is not so much the identification of species, as to provide a convenient means of summarizing the observed ranges in the character variants. Of course, species identification can be made simply by selecting certain of the more easily interpreted characters and determining the particular variant of each character which is found in the specimen or specimens at hand. In the case of the adult, the most easily interpreted characters are 1, 3, 6, 12, and 14. Few larvae have been described at the present time so that it is impossible to say what will be the most reliable characteristics. In the case of the two species described here, the form and chaetotaxy of the postscutum, and the position of s_1 (characters 1, 4, 10, 11, and 12) are the most easily applied. So far as the present data are concerned it must be remembered that the measurements shown in the tables of distribution of character variants in the case of the larva, are based upon the progeny of a single female, and the variation of the species as a whole must be greater than that shown in the table. In the case of the adult only one specimen in each case was involved; where a range is indicated, this is based on the variation on right and left sides of the one specimen. This is admittedly undesirable from the standpoint of an analysis of variation in the species, but at least it is a beginning and shows the probable direction which future attempts at the measurement and expression of interspecific and intraspecific variation should take in *Paratrombium* and related genera.

Characters such as the number of setae on each anterolateral lobe of the scutum of the adult are likely to be quite variable and to show intergradation between similar species. Nevertheless, it is obvious that the number of setae on the scutum will still be of value in separating species which are markedly dissimilar with respect to this character. The same is true of such characters as the number of setae on the genital and paragenital sclerites, the number of eupathidia on the palpal tarsus, and the proportions of tarsus I and tibia I. Characters dealing with the positions of setae on the leg segments have seldom been used in the differentiation of species, nor should they be used critically unless some work has been done to assess their variability in a series of specimens. A study of characters 4, 5, 6, 7, and 8, dealing respectively with the positions of s_1, e_d of tarsus I, f_1, s_2, and f_2, shows that in all of these cases the distribution of these setae overlaps in the two species. However, the mean positions show some variations which are certainly significant for the material studied, and probably for the species as a whole. Thus, while f_1 and e_d are at essentially the same level in the two lots of larvae studied, s_1 is considerably more distally placed in *P. bidactylus*, and the range in position of this seta in the two species barely overlaps. The same tendency toward distal placement of s_2 and f_2 in *P. bidactylus* is also seen, although the ranges overlap more than in the case of s_1.

In the tables of distribution of character variants, those variants given by Feider (1952) for *Paratrombium divisipilli* Feider 1948 (*P. d.*) are included wherever possible [here I use the name *P. divisipilli* as a specific rather than a varietal name, since it appears possible that *P. insulare* (Berlese) 1910 and Feider's form may eventually prove to be distinct species]. Where superscripts are given, these indicate the number of measurements on which a given range and mean are based.

SUMMARY OF CHARACTERS AND VARIANTS IN ADULTS OF *Paratrombium*

1a. Sensilla smooth (Fig. 77).
1b. Sensilla distinctly barbed (Fig. 76).
2. Number of setae on each anterolateral lobe of scutum (from constriction anterior to area sensilligera to anterior extremity, and omitting the medial setae).
3a. Posterior end of crista metopica distinctly swollen (Fig. 20).
3b. Posterior end of crista metopica not swollen (Fig. 50).
4. Number of setae on each genital sclerite.
5. Number of setae on each paragenital sclerite.
6a. Row of denticles on tarsus of chelicera distinctly bent near the middle (Fig. 22).
6b. Row of denticles on tarsus of chelicera forming a straight line (Fig. 55).
7. Position of solenidion of palpal tarsus.
8. Number of eupathidia on palpal tarsus.
9. Length of tarsus I, female.
10. Height of tarsus I, female.
11. Length of tibia I, female.
12. Length/height, tarsus I, female.
13. Tarsus I/tibia I, female.
14a. Hysterosomal setae tapering uniformly, peripectinate (Figs. 3–7).
14b. Hysterosomal setae rounded distally, clavate, peripectinate (as in *Paratrombium insulare* Berlese 1910).
14c. Hysterosomal setae diclavate, i.e., essentially clavate, but deeply bifid (as in *P. divisipilli* Feider 1948).
15. Body length, by sex.

SUMMARY OF CHARACTERS AND VARIANTS IN LARVAE OF *Paratrombium*

1a. Postscutum with two setae in normal individuals.
1b. Postscutum with four setae in normal individuals.
2. Total number of postscutal and postcoxal setae.
3a. Palpal tarsus with only two minute, peglike setae terminally (oil immersion, Fig. 35).
3b. Palpal tarsus with four setae here (not distinct except in most favorable material).
4. Position of s_1.
5. Position of e_d on tarsus I.
6 Position of f_1.
7. Position of s_2.
8. Position of f_2.
9a. Posterior claw reduced to a minute vestige about 4 μ long.
9b. (Other variants?)
10. Length of scutum/length of postscutum.
11. Width of scutum/width of postscutum.
12. Width of postscutum/length of postscutum.
13. Width of scutum, μ.
14. Length of idiosoma of unengorged larva.

Paratrombium bidactylus, new species

FEMALE: Idiosoma 1820 μ long to tip of scutum, 1118 μ wide, length/width 1.63. Scutum (Fig. 20) widest at anterior end, the width equal to .62 of the *median* length. The

DISTRIBUTION OF CHARACTER VARIANTS, ADULTS

	1	2	3	4	5	6	7	8	9
P. b.	a	22–25	a	37–39	26–29	a	.87–.92	11	486–491 μ
P. a.	b	13–14	b	48–55	ca. 55	b	.80–.85	17–19	423 μ
P. d.	b	?	a	?	?	?	?	?	454–474 μ (462)

	10	11	12	13	14	15
P. b.	153 μ	261 μ	3.24	1.86–1.90	a	1820 μ*
P. a.	144–149 μ	261–266 μ	2.84–2.94	1.59–1.62	a	1768 μ*
P. d.	?	232–261 μ (252)	?	(1.83)	b	♀ 1638–1885 μ (1816) ♂ 1085–1740 μ (1402)

* Based on females which had laid full complement of eggs.

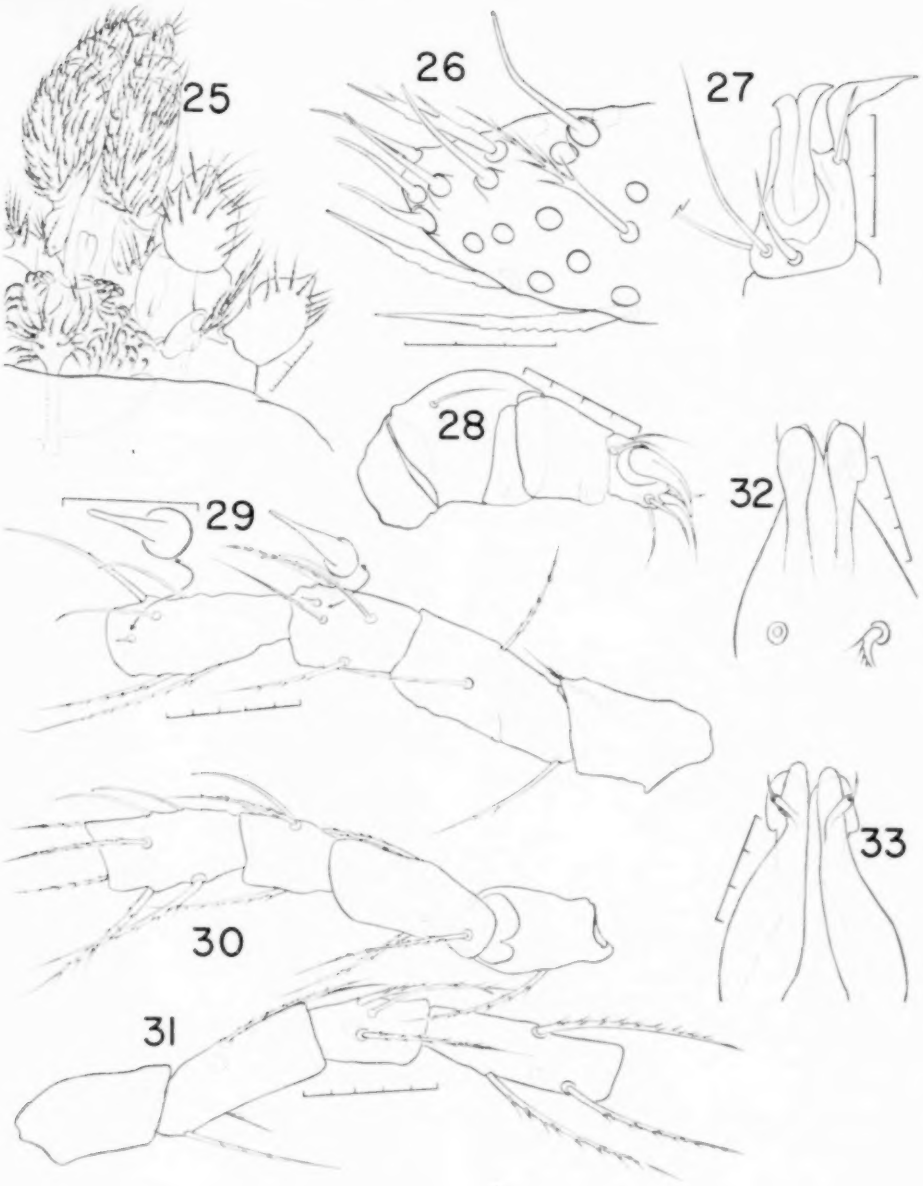
DISTRIBUTION OF CHARACTER VARIANTS, LARVAE

	1	2	3	4(s_1)	5(e_4)	6(f_1)	7(s_2)
P. b.	a	30	a	.47–.52(.49)[9]	.65–.71(.69)[9]	.45–.58(.53)[9]	.47–.54(.51)[10]
P. q.	b	32	b	.35–.48(.42)[10]	.64–.71(.66)[10]	.38–.55(.51)[10]	.40–.50(.45)[10]
P. d.	a	?	?	?	?	?	?

	8(f_2)	9	10	11	12	13	14
P. b.	.45–.55(.51)[10]	a	2.43[11]	1.09[11]	2.92[11]	216–236[11]	387–441 μ[10]
P. q.	.35–.49(.43)[10]	a	3.38[9]	1.23[9]	3.51[9]	188–208[9]	356–383 μ[5]
P. d.	?	a	2.76[1]	?	2.15	(compressed)	331–351 μ

anterolateral lobes of the scutum, extending from the anterior end to .21 are well developed, bearing 22 to 25 setae on each side, most of which are concentrated on the lateral arms. Sensilla situated at .39, appearing completely smooth even at magnifications of 1000× (oil immersion). Beginning at .32 and extending anteriorly is a deep furrow which widens gradually as it approaches the anterior margin of the scutum; at about .05 this furrow widens abruptly and disappears on the general surface of the scutum. In the specimen studied, there are three setae at the level at which the furrow disappears. Behind the constriction at .21, the scutum widens perceptibly around the area sensilligera and then tapers gradually toward the posterior end. At .79, the scutum is reduced to the thickness of the crista metopica alone. The crista is distinctly swollen between .90 and 1.0, with pigmented cuticle completely encircling the depression in the end of the crista. In the portion of the scutum between .21 and .79, there are 31 elongate peripectinate setae similar in form to those on the anterior portion of the scutum. In the specimen examined, 16 of these are on the left side and 15 on the right side. The marked indentation at .27 in the specimen from which Figure 20 was drawn was absent from the other side of the scutum. The elongate peripectinate setae on the surface of the propodosoma lateral to the scutum are borne on subconical papillae as are those on the hysterosoma. Ocular plates pedunculate, bicorneate. Anterior margin of hysterosoma projecting well beyond the posterior margin of the propodosoma so that the posterior portion of the scutum is hidden in dorsal view; setae along anterior margin of hysterosoma somewhat more slender and also smoother than those covering the rest of the body. Otherwise the setae of the hysterosoma are all of one type, heavily barbed, peripectinate, and the alveoli are at the apex of truncate conical papillae.

Setae of coxae I and II fairly stiff, peripectinate for about three-fourths their length, then smooth out to the usually rounded tips. Pars medialis coxae of rather unusual form, arising from inner angles of coxae I, and forming a narrow border about 15 μ wide around the convex inner angle of coxae II. The pars of right and left side are contiguous medially and may even appear to be fused in undissected specimens (Fig. 19). The pars medialis coxae contain 5 to 8 setae each, and because of their close approximation, the intercoxal area is completely isolated from the membranous cuticle behind the coxae; it contains between 25 and 40 closely packed peripectinate setae, somewhat shorter and thicker than the ones behind coxae II. Supracoxal seta slender, smooth; coxal ring of I and II both open dorsally. Membranous cuticle between coxae II and III apparently devoid of sclerites. Coxae III and IV as shown in Figure 24, coxal rings complete dorsally. No trace of a *Lawsenia*-organ was seen at coxa III although the dense vestiture may have concealed it. Genital and paragenital sclerites both well developed (Fig. 2); genital sclerites with 48 to 55 peripectinate setae each, the paragenital sclerites with about 56 setae each. Most of the setae have four to six whorls of barbs



FIGS. 25–26. *Paratrombium bidactylus*, n. sp., female: 25, propodosoma, dorsal; 26, tarsus of palp, anterior.

FIGS. 27–33. *Paratrombium bidactylus*, n. sp., larva: 27, tibia and tarsus of palp, dorsal; 28, entire palp, anterior; 29, trochanter to tibia I; 30, trochanter to tibia II; 31, trochanter to tibia III; 32, tip of rostrum, ventral; 33, same, dorsal.

each, but one or two of the setae at the posterior end of the genital sclerites are very nearly smooth. Three pairs of genital acetabula placed well back in the genital opening, decreasing in size from anterior to posterior. Anal sclerites present, but so well concealed by surrounding setae that their form and chaetotaxy were not ascertainable. Ventral hysterosomal setae arising from truncate, conical sclerites (Fig. 3).

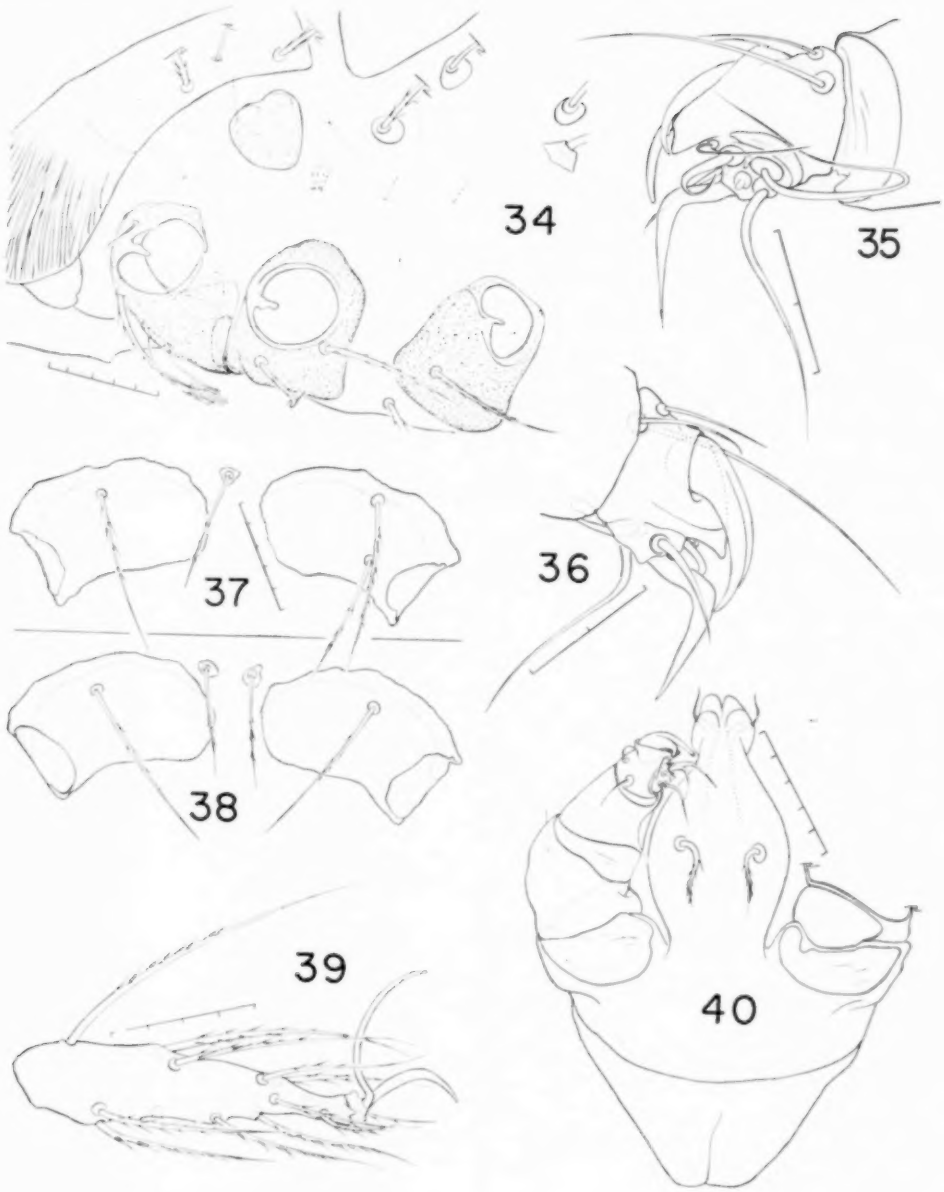
Base of gnathosoma with posterior ventral margin deeply concave; both base and rostrum with numerous curved, peripectinate setae. Velum simple, circular in outline, containing a central circlet of converging fimbriae. Four or five very slender, sparsely peripectinate setae arising from distidorsal surface of rostrum, and extending beyond the tip of the rostrum. Four or five setae arranged in a diagonal row posterolaterally to the velum. On the ventrolateral aspect of the rostrum are blunt setae, roughly rounded and smooth at the tips (Fig. 21).

Chelicerae (Figs. 22, 23) arched dorsally, fairly straight along the ventral margin. Dorsal membrane well developed and blunt. Tarsus of chelicerae with a row of 8 to 10 dorsal teeth in the distal half; at about the middle of the dorsal margin the row of teeth bends sharply down over the side of the tarsus where an additional 12 or 13 teeth of progressively diminishing size are found. Trochanter of palp with 9 or 10 elongate peripectinate setae in a fairly straight row down the posterior surface of the segment; anterior surface of trochanter bare, distal margin distinctly excavated. Odontus of tibia very heavy, undivided. Setae of tibia ranging from nearly smooth on anterior and posterior surfaces to very heavy and serrate along the dorsal margins. It is not known whether these setae are primarily serrate, or whether this condition arises as a result of a wearing or breaking off of the barbs. All of the setae of the tibia, with the exception of the odontus, are long, slender, and fairly flexible; no ctenidium is present. Each palpal tarsus in the specimen studied with 11 eupathidia ranging from .56 or .68*d* to .95 or .96*t*; the solenidia lie at .87 to .92*p* (one on each tarsus). The striated appearance of the solenidion is apparent only under favorable conditions.

Tarsus I 486–495 μ long, 153 μ high, length/height 3.24; tibia I 261 μ long, tarsus I/tibia I 1.86–1.90 (one specimen).

LARVA: Idiosoma (Figs. 41, 44) 387 to 441 μ long, 225 to 252 μ wide, length/width 1.73 to 1.88; average of 10 unengorged larvae 419 by 234 μ, length/width 1.80. Anterior margin of scutum truncate, with two heavy setae inserted dorsally just behind the margin; rostrum and palpi extending beyond the margin of the scutum. Just anterior to the level of coxa I is a prominent suture on either side of the scutum, these sutures not quite reaching to the lateral margin. Anterior to the sutures the margin of the scutum is characteristically marked by undulating striae. The remainder of the scutum is densely and uniformly punctate. Sensilla and the neighboring setae faintly barbed, the prosensillar setae completely smooth. Postscutum virtually as wide as the scutum (average ratio 1.09, 11 specimens), faintly punctate, bearing a pair of setae behind the middle of the plate. Ocular plates very small, bicorneate, completely lateral in position. Including the setae of the postscutum, there are 24 peripectinate dorsal and marginal setae; venter with 6 peripectinate postcoxal setae, making a total of 30 postcoxal and postscutal setae. Except for setae of postscutum, all these are borne on individual sclerites which bear a few punctae. Membranous cuticle appearing smooth at low magnifications, but faintly striate at higher magnifications.

Coxa I with a greatly enlarged rakelike seta anteromedially, bearing 10 to 15 digitiform teeth, identical in form with corresponding seta of *P. quadriseta* n. sp. (Fig. 63); anterolateral seta of coxa I elongate, slender, peripectinate. Coxa I with an elongate, sharp supracoxal seta; II and III without such a seta. Urstigma large. Coxae II and III sep-



FIGS. 34–40. *Paratrombium bidactylus*, n. sp., larva: 34, propodosoma, lateral, showing apodemes and *Lauseni*a-organ; 35, tibia and tarsus of palp, posterior; 36, tibia and tarsus of palp, anterodorsal; 37, setal anomaly in coxa III; 38, normal chaetotaxy at level of coxa III; 39, tarsus III; 40, gnathosoma, ventral.

arated by a distinct interval of striated cuticle, bearing two and one setae respectively. Intercoxal area with a single pair of setae between III. In one specimen (Fig. 37) there was only one intercoxal seta, but coxa III of the left side bore a supernumerary seta in the posterolateral corner which evidently represented the displaced intercoxal seta. Postcoxal area with only three pairs of ventral and submarginal setae. Anal anlage very well developed. A small but distinct *Lassenia*-organ can be seen laterally between coxae II and III in good specimens; it is seen to best advantage in somewhat rotated individuals (Fig. 34). In the specimen drawn, the pore had a diameter of slightly more than 1 μ, and opened into a duct about 22 μ long, the inner end of which was slightly swollen. This is unquestionably the homologue of the same organ in *Lassenia* (Johnstonianidae) in which it is better developed. The function, if any, is unknown; it is not an apodeme.

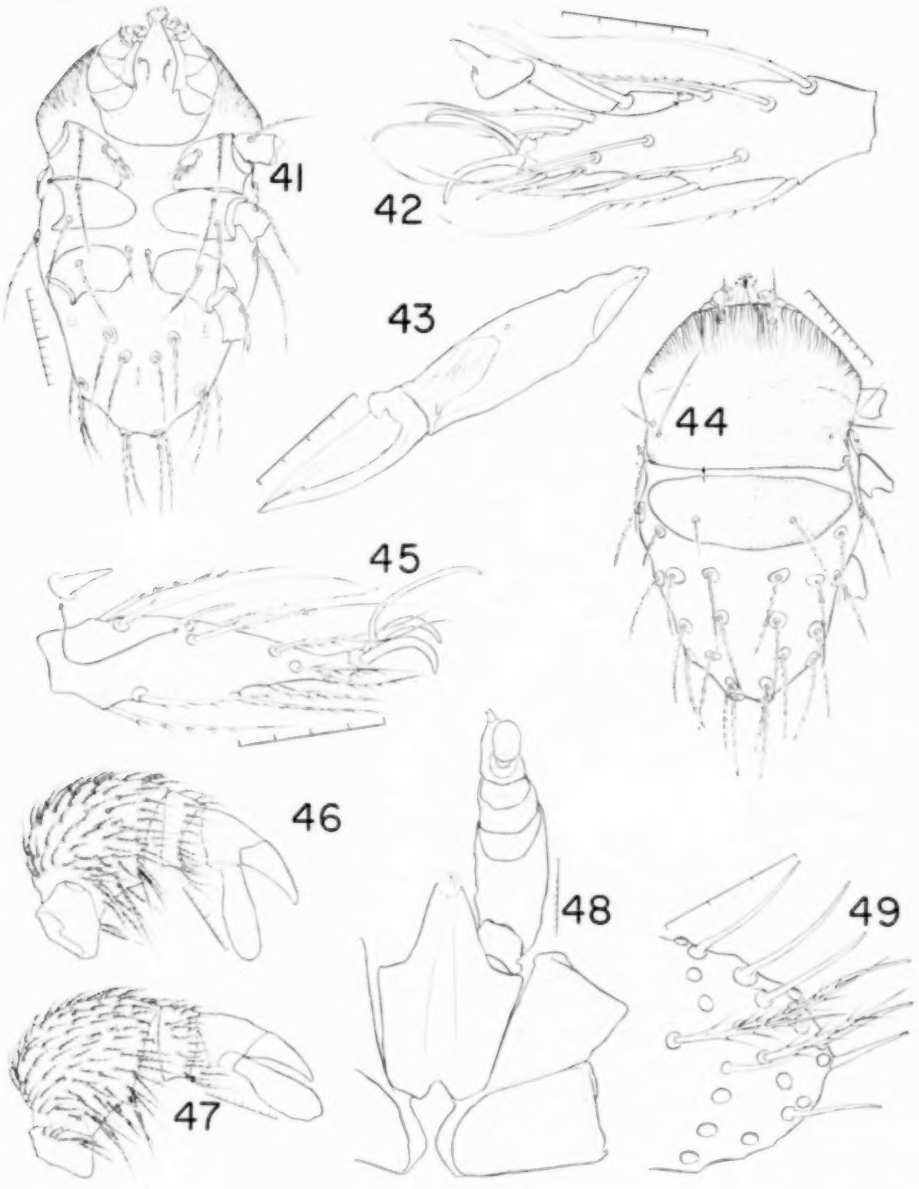
Base of gnathosoma with posterolateral margins converging to a rounded or truncate end posteriorly; devoid of setae, except for the minute spikelike supracoxal setae which are dorsal in position (Fig. 40). Protorostral setae smooth, inserted at the ends of a pair of characteristic tubular structures on the dorsal lobes of the velum. Deutorostral setae totally absent, tritorostral setae peripectinate, situated at about the widest part of the rostrum. Palpi five-segmented, but trochanter reduced to an ovate plate on the dorsal surface of the palp (see Fig. 72, *P. quadriseta*). The inner angle of the trochanter can be seen projecting beyond the anterior margin of the palp where at first it may appear to be a lobe on the femur (in Figure 40, the ventral portion of the left femur has been deleted to show the position of the trochanter). Femur with a smooth seta on dorsal surface, quite variable in position. Patella without setae. Tibia with three smooth setae plus the deeply cleft odontus; no specialized paradont. Tarsus reduced to a small cap on the anterior aspect of the tibia bearing only 7 setae (Fig. 35). These include the large apical L-shaped seta (possibly a modified eupathid?) plus 5 other normal setae of varying lengths and thicknesses. In the center is a minute peglike solenidion scarcely discernible even under oil immersion, plus one other seta of similar form. The palpi of this species are remarkable for the geniculate form, which considerably alters the normal morphological relationship of the palpi with the rostrum. The morphological dorsal line forms the lateral margin of the palp as seen in ventral or dorsal view.

Chaetotaxy of legs approximately as shown in table (s = solenidia, e = eupathidia, f = famulus, v = vestigial setae, c = companion setae, n = normal setae).

	tr	fe	pa			ti			ta				
	n	n	s	v	n	s	v	n	s	e	f	n	c
I	1	5, 6	2	1	4	2	1	5	1	2	1	17	0
II	1	4	1	1	3	2	0	5	1	0	1	14	0
III	1	4	1	0	3	0	0	5	0	0	0	13	0

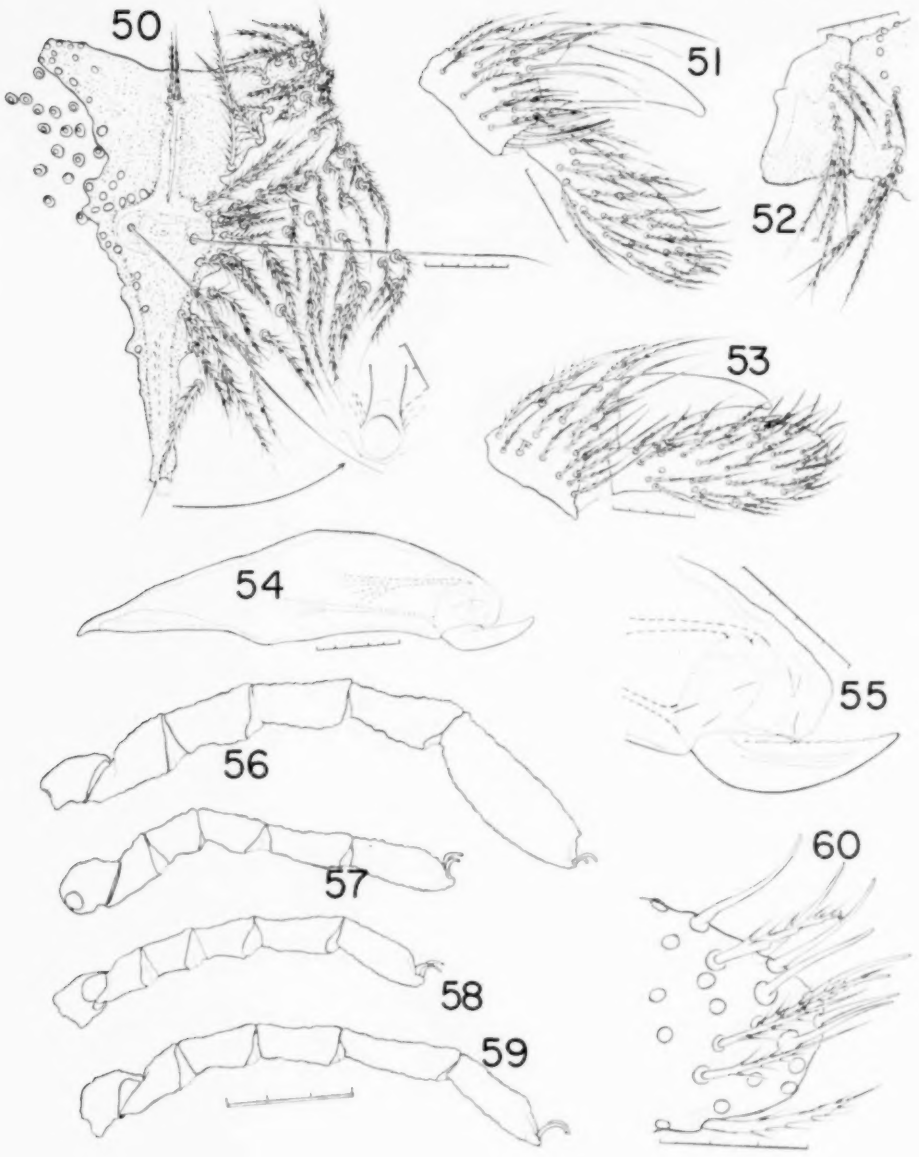
Basifemur and telofemur of all legs fused. Patella I with solenidia at .28 and .45*d*, II and III with solenidia at .34 and .39*d*, respectively. Patella I and II each with a solenidion at .79 and .77*d*, respectively. Tibia I with solenidia at .56 and .75*d*, a vestigial seta at .90*pd*; II with solenidia at .39 and .56. The solenidia of the tibia show no readily perceptible difference in form. Tarsus I with S_1 at .47 to .52, a dorsal eupathid (e_d) at .65 to .71*d*, and a famulus at .45*d* to .58*d*. Tarsus II with S_2 at .47 to .54*pd* and f_2 at .45–.55; III with no specialized setae. Other chaetotactic features as shown in table. Tarsi I and II with three claws each, the median claw more slender than the anterior and posterior claws; III with posterior claw reduced to a minute vestige about 4 μ in length as in the case of *P. quadriseta* n. sp. (Fig. 74).

TYPE LOCALITY: Sherwood Creek, Mason



FIGS. 41–45. *Paratrombium bidactylus*, n. sp., larva: 41, venter; 42, tarsus I, posterior; 43, chelicera; 44, dorsum; 45, tarsus II, posterior.

FIGS. 46–49. *Paratrombium quadriseta*, n. sp., female: 46, palp, anterior; 47, palp, posterior; 48, outline of propodosoma and gnathosoma, ventral; 49, detail of end of palpal tarsus, posterior.



FIGS. 50–60. *Paratrombium quadriseta*, n. sp., female: 50, scutum of dissected specimen; 51, tibia and tarsus of palp, anterior; 52, trochanter of palp, posterior; 53, tibia and tarsus of palp, posterior; 54, chelicera; 55, tarsus of chelicera; 56–59, legs I–IV; 60, tip of palpal tarsus, anterior.

County, Washington. Sandy mud, in grass. July 27, 1954. Collected by the writer. At the point where this species was found, Sherwood Creek is estuarine, opening into Case Inlet of Puget Sound. The mites were collected on a low mound which was nearly covered by high tide.

REMARKS: The correlation between the larva and adult described above was established by rearing from eggs laid by the female collected at the type locality.

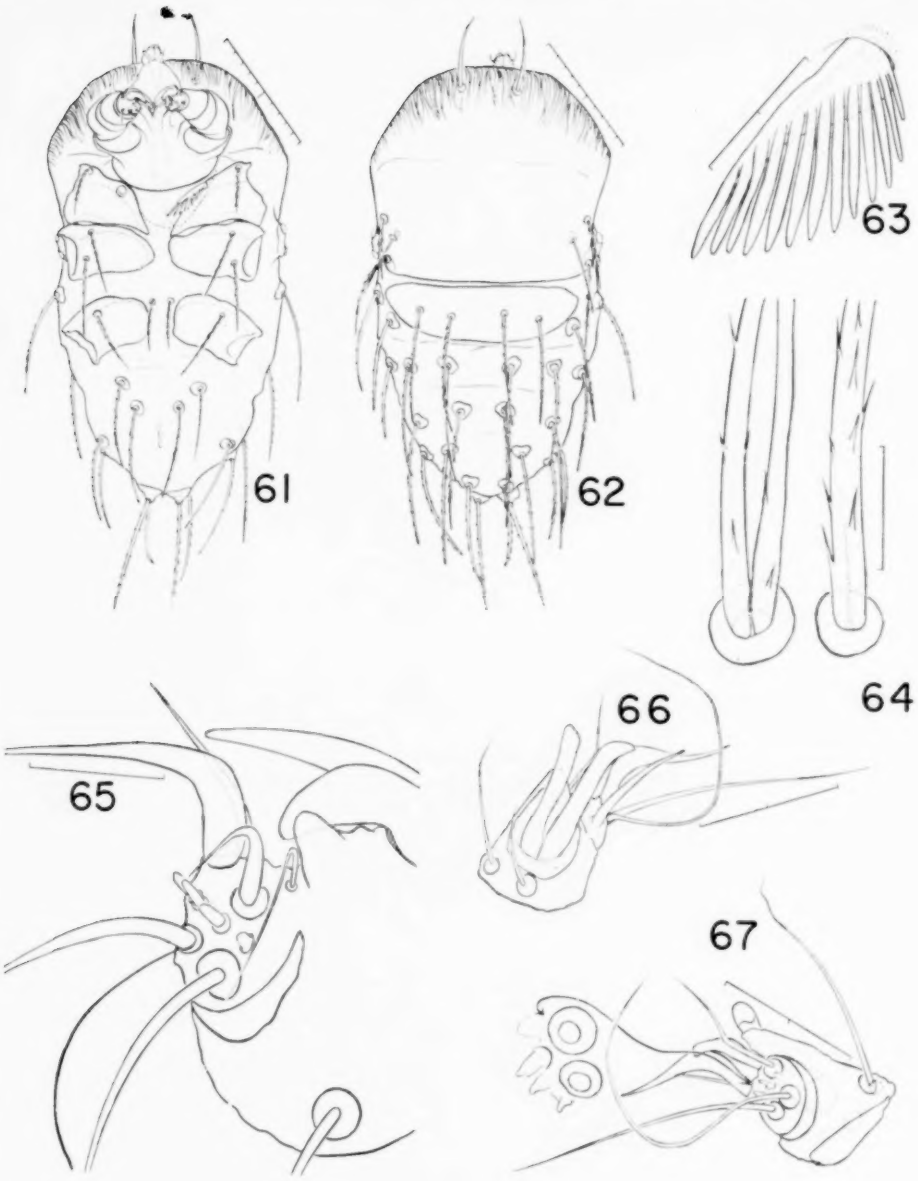
The relationship of this species to described forms is somewhat obscure, but there is no doubt that it is congeneric with *P. quadriseta* n. sp. The adult keys out with some slight inconsistencies to the genus *Caenothrombium* Oudemans, 1927, and agrees with the type of that genus in a number of details, including the general form of the crista, the double, stalked eyes and the absence of a distinct ctenidium on the tibia of the palp (there is definitely no distinct ctenidium in *P. b.* and *apparently* none in *C. caloris*). However, the larva does not appear to be congeneric with the larva of *C. miniatum* Womersley, 1934, for which species Womersley has established a correlation. Differences, as far as can be judged from Womersley's figures of this larva (1939*a*: 156), are in the chaetotaxy of the scutum, the absence of the heavy comblike seta of coxa I and the undivided (?) odontus. The drawings in the original description of the larva are not complete, but they probably are fairly accurate in these three respects. The larva of *P. bidactylus* keys out to the third dichotomy in the key given by Thor and Willmann (1947: 484). At this point further separation was made on the basis of the claws of tarsus III—whether these are normal, or whether the posterior claw (inner-claw) is deformed. Neither of these fits *P. bidactylus* or *P. quadriseta* accurately, and the key, as well as the diagnosis of the genus given by Thor and Willmann, were in error on this point. The fourth dichotomy of that key is totally unreliable since it is based upon the presence or absence of setigerous sclerites behind the postscutum. It is quite likely that these have been overlooked by many authors in describing their species because of refractive index difficulties.

An examination of the drawings of the larva of *P. egregium* presented by Bruyant, Oudemans, and Thor and Willmann shows a close similarity between *P. bidactylus* and *P. egregium* Bruyant, 1910. The similarity is indicated in the shape of the scutum, the form of the prosensillar setae and their insertion at the ends of long canals, the heavy pectinate tritorostral setae, the comblike seta of coxa I and the chaetotaxy of the body, especially the ventral setae. These forms are extremely similar, and the resemblance is far too close to be a consequence of convergence; hence we can assume that they are actually very closely related.

The foregoing discussion leaves a number of important questions. For one thing, is the genus *Caenothrombium* made up of generically related species, or is it a composite? Was Womersley correct in assigning his *Caenothrombium miniatum* to that genus? Was the female which laid the eggs from which Womersley described the larva actually *C. miniatum* or a different species? There seems to be no way in which these questions can be resolved by reference to the literature, so further speculation about them is pointless.

Paratrombium quadriseta, new species

FEMALE: Idiosoma, 1,768 μ long to tip of scutum, 1,092 μ wide, length/width 1.62. Scutum of dissected female (Fig. 50) resembling that of *P. bidactylus* in most details. However, the anterolateral lobes of the scutum, extending from about .25 to the anterior limits of the scutum bear only 13 to 14 setae on each side (*P. b.*: 22 to 25 setae on each side). In the present species there is a wide interval between the three anteromedian setae and those more laterally placed, whereas in *P. bidactylus*, this wide gap was not found. Width of scutum equal to .67 of the *median* length. Sensilla situated at .40, appearing



FIGS. 61–67. *Paratrombium quadriseta*, n. sp., larva: 61, venter; 62, dorsum; 63, medial seta of coxa I; 64, anomalous postscutal seta and normal homologue; 65, tibia and tarsus of palp, posterior; 66, tibia and tarsus of palp, dorsal; 67, tibia and tarsus of palp, posteroventral.

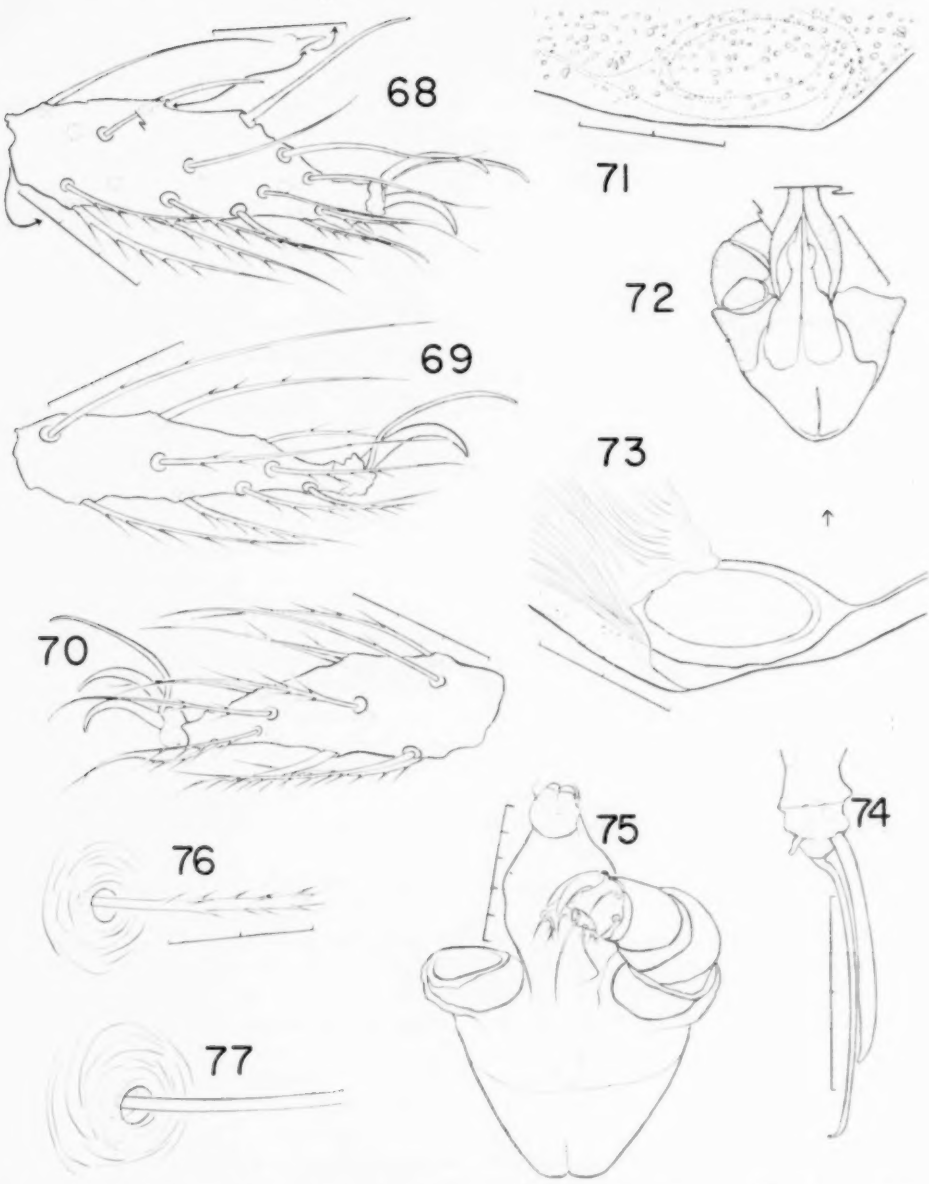
minutely barbed at magnifications of 600 × (Fig. 76). Beginning at .32 and extending anteriorly is a deep furrow, reaching to the level of about .08; beyond this level are three setae as in the previous species. Narrowest point of scutum at .22 to .27. Punctate cuticle extending very nearly to the posterior end of the scutum, which is not markedly swollen as in *P. bidactylus*, and the pigmented cuticle ends in front of the depression in the end of the crista. In the portion of the scutum between .25 and .68 of the specimen examined, there were 30 setae, 15 on each side (*P. b.*: 31 setae here, in the one specimen). Crista metopica tapering somewhat more gradually behind area sensilligera than in preceding species. Ocular plates and dorsal hysterosomal setae as in *P. bidactylus*.

Ventral surface of the body showing no significant differences from *P. bidactylus*, except for a slightly more sparse vestiture of the coxae and genital sclerites. Genital sclerites bearing 39 and 37 setae (*P. b.*:48–55), paragenital sclerites bearing 26 and 29 setae (*P. b.*: about 55 on each side). The form of these setae is essentially identical in the two species, however. Gnathosoma in ventral view resembling that of *P. bidactylus*, but slightly larger; rostrum not reaching to distiventral margin of femur (in *P. bidactylus* the rostrum extends to a point about half way between the distiventral and distidorsal margins of the segment).

Chelicerae virtually identical with those of *P. bidactylus*, except that the row of denticles is straight throughout its length, whereas in the preceding species it is sharply deflected about the middle. Palpi virtually identical in general size and form with those of the preceding species. Tibia with large unidentate odontus but without paradont. One feebly developed ctenidium present, consisting of about four setae somewhat longer, heavier, and smoother than the others, extending along the anteroventral margin at the insertion of the tarsus. Eupathidia of tarsus extending from .68*d* to .95*v*, solenidion at .80 to .85*p*. The eupathidia of the palpal tarsus of this species are noticeably more numerous (17–19) than in *P. bidactylus* which has only 11 on each tarsus. With such a difference as this, it is doubtful that study of larger numbers of individuals would show much overlapping in this character.

Tarsus I 423 μ long, 144–149 μ high, length/height 2.84–2.94; tibia I 261–266 μ long, tarsus I/tibia I 1.59–1.62 (single specimen).

LARVA: Idiosoma (Figs. 61, 62) 356 to 383 μ long, 189 to 203 μ wide, length/width 1.87 to 1.92; average 374 μ by 197 μ, length/width 1.88 (five unengorged larvae). Scutum essentially as in *Paratrombium bidactylus;* prosensillar setae completely smooth, somewhat spindle-shaped, with thickest portion about one-fourth of the way out on the shaft. Anterior portion of scutum striate, posterior portion densely and uniformly punctate. Sensilla appearing smooth at low magnifications but faintly pectinate under higher magnifications. Ocular plates bicorneate, the anterior cornea larger than the posterior. Postscutum bearing four setae in a transverse row. (In some individuals of *P. bidactylus*, one of the setae of the postscutum may be duplicated, but in these cases the placement of the supernumerary seta is quite different since it is not aligned with the two normal setae.) Remaining dorsal and marginal setae identical in number and position with those of *P. bidactylus*, so that there is a total of 26; venter with 6 peripectinate postcoxal setae, making a total of 32 postcoxal and postscutal setae. Except for the setae of the postscutum, all of the setae are borne on individual punctate sclerites. Membranous cuticle faintly striate, but the striae do not make any striking pattern. Ventral surface showing no significant difference from *P. bidactylus*. One dissection provided considerable insight into the structure of the so-called urstigma (or "urpore"). In Figure 73 (dorsal view) the urstigma is seen to consist of an elliptical cavity or ring, with no opening whatever on the ventral sur-



FIGS. 68–75. *Paratrombium quadriseta*, n. sp., larva: 68, tarsus I, posterior; 69, tarsus III; 70, tarsus II; 71, urstigma, left coxa I, ventral; 72, outline of gnathosoma, dorsal; 73, urstigma, detached coxa I, dorsal; 74, tarsal claws III, right side, dorsal; 75, gnathosoma, ventral.

FIG. 76. *Paratrombium quadriseta*, n. sp., female, base of sensillum.

FIG. 77. *Paratrombium bidactylus*, n. sp., female, base of sensillum.

face (Fig. 71). The posterior wall of the urstigma lies in a slitlike pouch between the posterior margin of coxa I and the overlying membranous cuticle of the ventral body wall. An apodeme arises from the anterior margin and extends in an anterior direction. The punctate cuticle posterolateral to the urstigma in Figure 73 is the upturned margin of coxa I which continues directly with the striated membranous cuticle of the body wall. Although the function of the urstigma is not apparent from this, it obviously is not a respiratory opening. The term "urpore" is a misnomer, but "urstigma" appears to be acceptable as long as it is understood that it is not a "stigma" in the sense of a respiratory opening. Details of lateral portion of propodosoma as shown for *P. bidactylus* (Fig. 34). Base of gnathosoma as described for *P. bidactylus*, except that the supracoxal setae appear to be consistently more lateral in position, and also shorter and blunter. Palpi as in previously described species, except for chaetotaxy of tarsus. The tarsus bears four long setae dorsally, one of which is very slender, another heavy and scythe-shaped, and the other two intermediate in form. The two ventral setae are flexible and very elongate. Between the four dorsal and two ventral setae is a transverse row of four short, peglike setae. One of these is presumably the solenidion, probably the most posterior one, but all four are so similar in form and size that it is impossible to say for certain which one is the true solenidion. Podocephalic canals very short, extending scarcely to the level of the anterior margin of coxa I. Rostrum as in *P. bidactylus*.

Although the larva of *P. bidactylus* is larger than that of *P. quadriseta*, its palpal tarsus appears to be both actually and relatively smaller. In one specimen of each of the two species, the maximum diameter of the base of the tarsus measured 10 and 13 μ respectively, which is a considerable difference in a structure of this small size. In *P. quadriseta*, four small setae can be resolved with little or no difficulty, arranged in a straight row across the distiventral surface of the tarsus. In *P. bidactylus* on the other hand, only two setae can be seen with any certainty here, and these are noticeably compressed between the bases of the larger setae and the tarsus (Figs. 35, 67).

Femora I–III undivided, basiventral seta of all femora very delicate, only about half the diameter of the other setae on the segment. Chaetotaxy of legs similar to that of *P. bidactylus*, at least so far as the number of setae on the various segments is concerned. Solenidia of patella I at .37*d* and .54*d*, vestigial seta at .80*d*. Tibia I with solenidia at .50*d* and .74*d*, a vestigial seta at .88*d*. Tarsus I with solenidion at .35–.48*d*, e_d at .64–.71, and e_b at 0.94, famulus at .38–.55. Patella II with a single solenidion at .40, vestigial seta at .73; tibia with two solenidia, at .39*d* and .61*d*. Tarsus II with solenidion at .40–.50*d*, famulus at .35–.49*d*; eupathidia lacking. Patella III with solenidion at .47, tibia without solenidia. Tarsus III typically bears four whorls of normal setae containing three, four, four, and two setae each (total 13), but of 8 tarsi examined, two had 14 normal setae and one had 12 normal setae. The basal whorl normally contains only three setae, but in exceptional specimens a fourth has been added. In that tarsus III with only 12 setae, the deletion occurred in the third whorl from the base of the tarsus. Tarsi I and II each has three well-developed claws, the median one more delicate and erect than the anterior and posterior claws. Tarsus III with anterior and median claw well developed, posterior claw as in *P. bidactylus*, reduced to a very minute rudiment.

TYPE LOCALITY: Riverside, California, Santa Ana River, at Camp Evans. Females found crawling on muddy bank of stream, April 23, 1955. Collected by the writer.

REMARKS: The correlation between the larva and adult of this species was established by rearing. This species is obviously closely related to *Paratrombium bidactylus*, but the dif-

ferences between them appear to be of truly specific nature. They can be differentiated immediately on the basis of the chaetotaxy of the postscutum. In view of the variation noted in *P. bidactylus* it should be expected that exceptional forms might be found which have four setae on the postscutum, although none has been seen by the writer. However, even if this were to occur, the position of the lateral setae in *P. quadriseta* is very characteristic, these forming nearly a straight line with the medial setae. There are other differences too, of a more relative nature, in the proportions of the scutum and postscutum and the positions occupied by the specialized setae of tarsi I and II. These are summarized in the preceding table of variants of larval characters.

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